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(Founded by G. H. F. Nuttall, F.R.S.)

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THE ANATOMY OF *ANTHOBOTHRIUM AURICULATUM* (RUD.) (CESTODA) FROM *RAJA BATIS* L.

BY GWENDOLEN REES, D.Sc., *Department of Zoology, University College of Wales, Aberystwyth*

(With 17 Figures in the Text)

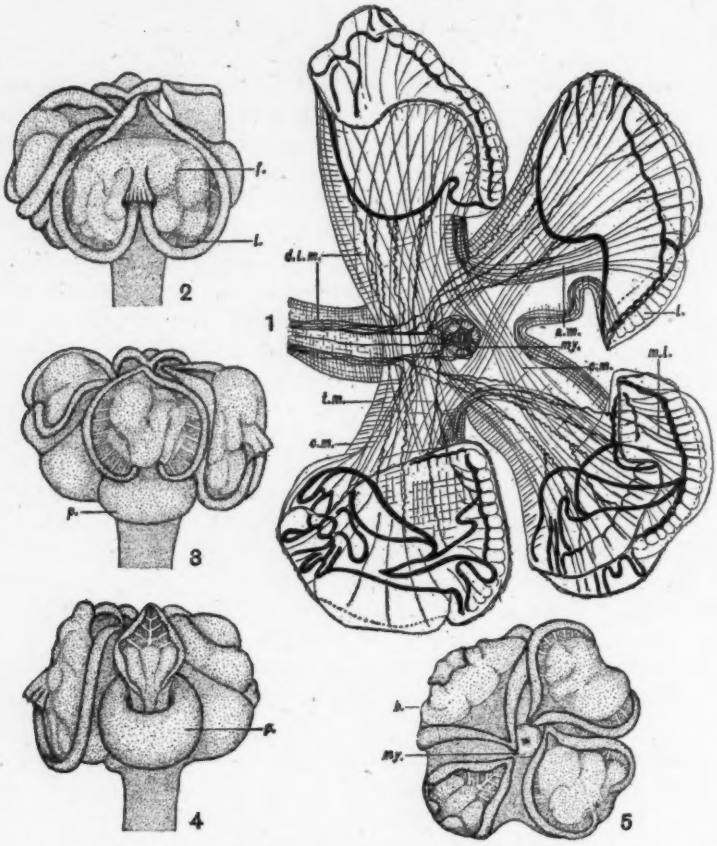
161 *Anthobothrium auriculatum* (Rud.) is often referred to as 'an insufficiently known species'. 167 Southwell (1925) states that 'all that is known about this doubtful species is contained 173 in Rudolphi's brief description, which is quite insufficient to diagnose the species with certainty'. Rudolphi (1819) first described it as *Bothriocephalus auriculatus* from *Torpedo marmorata* Risso; it is possible that this brief and inadequate description included 178 several species. Leuckart (1820) described what has since been regarded as the same species under the name of *Bothriocephalus flos* from *Carcharinus glaucus* (L.), Bremser 180 (1824) gave a brief account of *Bothriocephalus auriculatus*, and Zschokke (1888) gave a somewhat fuller account of *Anthobothrium auriculatum* from *Torpedo marmorata*. As 186 far as can be judged all these forms are synonymous. Diesing (1850) described what he thought to be Rudolphi's species, placing it in the genus *Tetrabothrium*; he obtained it from *Torpedo marmorata* Risso, *Hexanchus griseus* (Gm.), *Carcharinus glaucus* (L.), *Squatina squatina* (L.), and *Raja calvata* L. It has been pointed out by several writers 197 that Diesing's *Tetrabothrium auriculatum* does not agree with *Anthobothrium auriculatum* (Rud.), because, among other things, the genital pores in the former are anterior and in 207 the latter posterior. Southwell (1925) states that Beauchamp is of the opinion that *Tetrabothrium auriculatum* Dies. is synonymous with *Phyllobothrium gracile* Wedl., an idea which is now generally accepted. Joyeux & Baer (1936) recorded *Anthobothrium* 209 *auriculatum* (Rud.) fairly frequently in a number of host fishes, namely, *Mustelus mustelus* (L.), *Scyliorhinus caniculus* (L.), *Lamna cornubica* (Gm.), *Eugaleus galeus* (L.), *Squatina squatina* (L.), *Carcharias glaucus* (L.), *Torpedo marmorata* Risso, and *Raja clavata* L. 220 They, too, refer to the species as imperfectly known, and suggest that it might be synonymous with some other species of the same genus. In view of the lack of an 225 adequate description of *Anthobothrium auriculatum* it was felt that an account of its 226 anatomy would render future identification of the species simpler and would settle the question as to whether or not it was synonymous with some other known species.

Specimens were obtained from the intestine of *Raja batis* L. caught in the deep-sea fishing grounds on the Porcupine Bank to the west of Ireland. It has not previously been recorded from this host. The worms were fixed in Gilson's fluid. Anatomical details have been worked out from in toto mounts, and serial sections cut from 5 to 8μ in thickness and stained with Ehrlich's haematoxylin and either orange G or eosin.

SCOLEX

The scolex bears two dorsal and two ventral pedunculate bothridia, the degree of expansion and contraction of which determines the variable form of the scolex. In the expanded condition (Fig. 1) each consists of a stalk or peduncle measuring 0·66–1·11 mm. in length and 0·95 mm. in breadth at the apex; the peduncle narrows slightly towards

the base. The apex bears a funnel-shaped or auriculate expansion (Figs. 6, 7) measuring up to 2 mm. in diameter, the margin of which is much complicated by folding and by the development of small rather indefinite loculi along part of its length. The apex of the 'funnel' is pointed and directed anteriorly (Fig. 5), the remainder of its margin is more or less rounded in outline. The 'funnel' itself is delicate and membranous and the margin edged by a narrow frilled expansion of cuticle (Figs. 6, 7). A short distance behind the

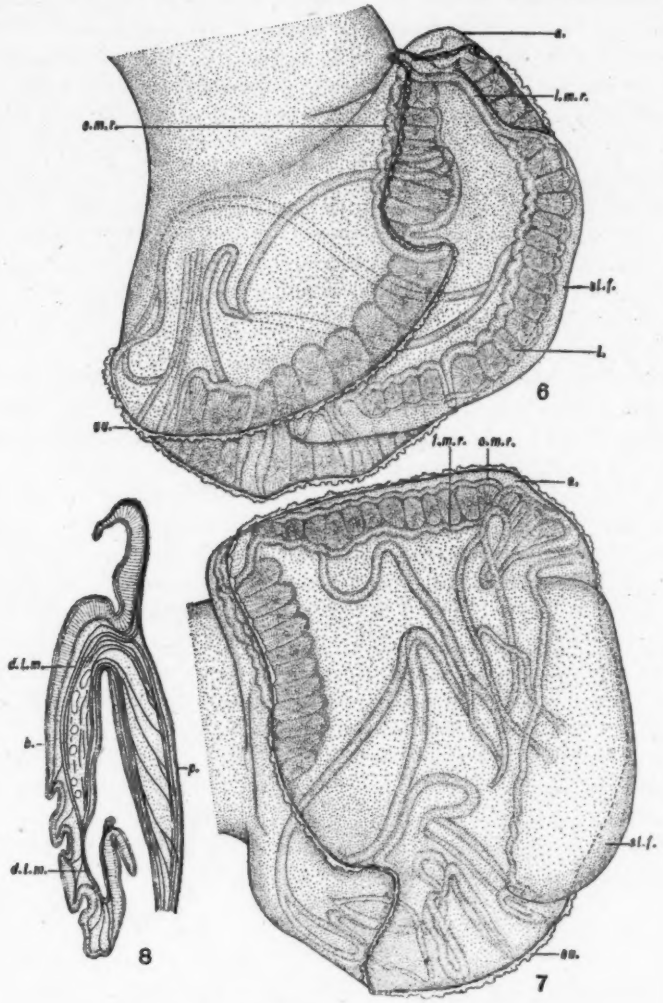


Figs. 1–5. *Anthobothrium auriculatum* (Rud.).

Fig. 1. Expanded scolex showing main arrangement of muscles; simplified for clarity.
Figs. 2–4. Scolex showing bothridia in various stages of contraction.
Fig. 5. Terminal view of scolex showing myzorhynchus.

apex and on the left side only there is in each bothridium a delicate semilunar fold extending for a short distance, backwards, inside and parallel to the margin of the 'funnel'. It is fused along its base to the inside of the funnel wall and extends a little beyond the margin at its widest part, giving the wall a double appearance in this region. The funnel is supported by thickened muscular ridges which are for the most part constant in arrangement. From the apex there extends backwards along each side close to

the margin a muscular ridge which is prominent in the early part of its course but later gradually becomes less distinct until it finally disappears. The ridge on the right margin is a little better developed than the ridge on the left. Some little distance within this



Figs. 6–8. *Anthobothrium auriculatum* (Rud.).

Fig. 6. Expanded bothridium partially folded over.
Fig. 7. Expanded bothridium opened out.
Fig. 8. Longitudinal section of expanded bothridium showing insertion of deep longitudinal muscles on muscular ridge.

ridge and parallel to it is another ridge on each side. On the left side it marks the base of the semilunar fold and its line of fusion to the inside of the funnel wall. These ridges, too, gradually diminish as they pass backwards. The fold itself bears a ridge near its

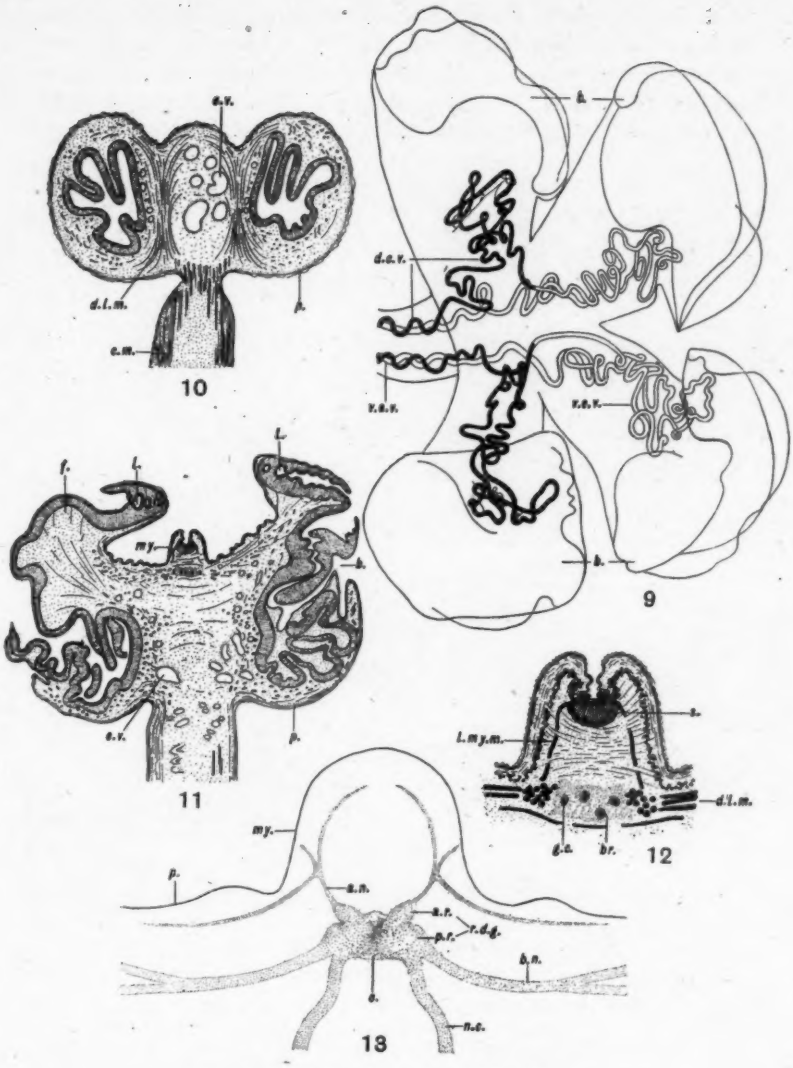
free outer border which seems to be the result of the bifurcation of the inner marginal ridge at the point of origin of the fold. The inner and outer marginal ridges on each side are connected by a series of transverse ridges forming a row of rather indefinite oval loculi (Figs. 6, 7). They can hardly be described as loculi, as the intervening walls are formed from longitudinal muscles passing up from the peduncle; the prominence of the loculi therefore depends on the degree of contraction of these muscles. On the right margin there are about fourteen fairly well-defined loculi followed by twelve more which are much less clearly defined. On the left side there is about the same number, but the arrangement is further complicated by the semilunar fold. Loculi also occur on the outer side of the fold and correspond in position and number to those on the inner side of the 'funnel' in this region. There are about seventeen on the outer side of the fold and twenty-eight on the inner side of the funnel. The posterior margin of the bothridium is devoid of loculi; the wall here is thin, membranous and folded and is provided with supporting muscular ridges radiating outwards towards the margin. The floor of the bothridium is also provided with a series of muscular ridges which are more or less constant in arrangement.

The appearance of the contracted bothridium is very different from that of the expanded. During contraction the bothridium at first assumes a heart-shaped outline 1·8 mm. broad and 1·43 mm. long (Fig. 2), the pointed apex becoming more pronounced and the membranous base being folded inwards (Fig. 11). The margin of the 'heart' is formed by the thickened muscular ridges, the posterior ends of which are brought together and turned inwards by the action of contracting muscle fibres. As the peduncle is also contracted the floor of the 'funnel' is now a raised cushion traversed by grooves which are the contracted muscular ridges. The semilunar fold is not distinguishable but the loculi are more prominent (Fig. 2). Further contraction of the bothridium results in a further change in shape (Fig. 3). The posterior end becomes turned in still more so that the bothridium assumes the shape of an arrow head and the peduncle is almost globular (Fig. 4). The overall diameter of the contracted scolex and bothridia is 2·14 mm. as compared with the expanded overall measurement of 5·2 mm.

At the apex of the scolex is a small myzorhynchus (Figs. 1, 5, 11, 12). When contracted it appears as a small conical elevation 0·17 mm. long and 0·255 mm. broad at the base (Figs. 11, 12). When expanded it is club-shaped with a narrow base and measures 0·34 mm. in length. At the apex of the myzorhynchus there is a 'sucker', the cavity of which opens to the exterior by a small slit-like aperture (Fig. 1).

Strobila

The scolex is followed by a short neck 1·0 mm. long and 0·48 mm. broad, and a strobila measuring up to 100 mm. in length. The maximum breadth of 0·826 mm. is just in front of the posterior extremity. The anterior proglottides are very short and broad, measuring 0·037 mm. long and 0·55 mm. wide. Further back they become slightly longer relatively, and in the widest region measure 0·137 mm. long, and 0·826 mm. wide. The last few segments of the complete worm narrow slightly and are almost square in outline, measuring 0·367 mm. in length and 0·5 mm. in breadth (Fig. 14). The genital apertures are irregularly alternate and occur just behind the middle of the lateral margin.

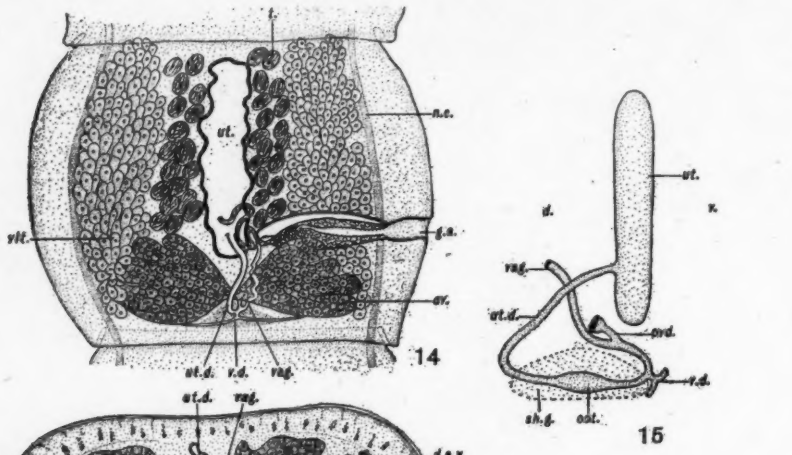


Figs. 9–13. *Anthobothrium auriculatum* (Rud.).

Fig. 9. Expanded scolex showing excretory system, dorsal view.
Fig. 10. Longitudinal section of contracted scolex showing course of deep longitudinal muscles.
Fig. 11. Median longitudinal section of contracted scolex showing myzorhynchus and infolding of basal part of bothridial funnel into bothridial peduncle.
Fig. 12. Median longitudinal section of myzorhynchus.
Fig. 13. Brain and nerves, dorsal view.

Musculature

(*a*) *Strobila.* The superficial musculature consists of very delicate outer circular and inner longitudinal layers lying immediately below the basement membrane (Fig. 10). The deeper musculature consists of longitudinal muscle bundles only. They form a broad band surrounding the strobila throughout its length (Fig. 16), and are better developed dorsally and ventrally than at the lateral margins. Each bundle consists of up to thirty



Figs. 14–17. *Anthobothrium auriculatum* (Rud.).

Fig. 14. Mature proglottid, dorsal view.
Fig. 15. Reconstruction of female genital ducts from side.
Fig. 16. Transverse section of mature proglottid in region of origin of oviduct.
Fig. 17. Cirrus sac and vagina, anterior view.

fibres, the larger ones being on the inside, and anastomosis of the fibres of adjacent bundles takes place. A few dorso-ventral fibres extend across the medullary region. There is no change in the musculature in the neck region except that the bundles are more uniform in size, and continue into the scolex to form the complicated musculature of the bothridia.

(*b*) *Scolex.* A delicate layer of superficial muscles surrounds each peduncle just beneath the basement membrane (Fig. 1). The superficial longitudinal muscles of the neck extend

forwards dorsally and ventrally on to the outer sides of the bothridia peduncles. They continue forwards just below the circular muscles spreading out fanwise and are inserted on the outer, or posterior, margin of each 'funnel'. The superficial muscles of the anterior faces of the peduncles are more complicated in arrangement, being probably more intimately concerned with the movements of the bothridia. They can be arranged under three headings: (1) Transverse muscles, which extend from the inner side of the right dorsal to the inner side of the left dorsal peduncle and similarly from the right ventral to the left ventral (Fig. 1). (2) Oblique muscles, which extend from the right dorsal to the left ventral and from the left dorsal to the right ventral peduncle. They therefore cross one another at the anterior extremity of the scolex curving around the myzorhynchus which is therefore surrounded by a ring of fibres at its base. (3) Adjacent muscles, which connect the dorsal peduncle with the ventral peduncle on each side respectively.

The fibres of each of these three series of muscles spread out fanwise at their extremities and cross one another, the general arrangement appearing extremely complicated. Within the cavity of the 'funnel' there is a delicate system of superficial muscles which cross one another at right angles (Fig. 1). Delicate circular muscles are present just at the base of the narrow frilled margin which surrounds the aperture of each bothridium (Figs. 6, 7).

The deep longitudinal muscles lie just below the superficial ones and take a somewhat similar course. As they emerge from the neck into the peduncles of the bothridia the deep longitudinal muscles divide into two layers; the outer layer passes up the outside of each bothridium just underneath the superficial muscles, and the inner layer continues straight forwards towards the apex of the scolex and there divides again, some of the fibres running up the inner face of each peduncle and the others passing across the apex of the scolex to become continuous with those from the opposite side (Fig. 11). From these latter, muscles go to the myzorhynchus (Figs. 1, 11, 12). Some of the deep longitudinal muscles are inserted on to the muscular ridges of the bothridia (Figs. 1, 8) and others form the partitions between the series of marginal loculi (Fig. 1). The bundles are larger than those of the superficial system, more widely separated from one another, and during contraction they are thrown into waves, a condition not apparent in the superficial system.

The floor of each loculus is provided with delicate fibres radiating from the centre (Figs. 6, 7), which play some part in changing the shape of the loculus.

(*c*) *Myzorhynchus.* At the apex of the myzorhynchus there is a sucker-like structure opening to the exterior by a small slit-like aperture (Fig. 12). The sucker measures 0·074 mm. in transverse diameter and 0·04 mm. in depth. It has a muscular wall composed of radial muscle fibres and its cavity is lined by cuticle continuous with that covering the surface of the body. The wall of the myzorhynchus is provided with superficial circular and longitudinal muscles which help in its contraction and expansion. From the deep longitudinal muscles which cross over at the apex of the scolex originate fibres which extend upwards into the myzorhynchus forming well-developed bundles which are inserted in a ring on to the outer side of the terminal sucker (Figs. 1, 12). Contraction of these fibres serves to pull in the sucker and to shorten the myzorhynchus.

(*d*) *Cirrus and vagina.* In the mature segments some of the dorso-ventral muscle fibres in the region of the genital ducts are inserted on to the walls of the cirrus sac and

vagina. These are most prominent just internal to the genital atrium, but a second group is inserted on the vagina at its internal extremity (Fig. 17). Contraction of these fibres serves to enlarge the cavities of the ducts and may help in the protrusion of the cirrus.

Nervous system

The nervous system which is very simple (Fig. 13) consists of a brain, two lateral nerve cords, anterior nerves arising from the brain supplying the myzorhynchus and anterior surface of the scolex, and bothridial nerves supplying the bothridia.

The brain is situated at the anterior end of the scolex just below the myzorhynchus. It is dorso-ventrally compressed and consists of a ganglionated mass not distinguishable into very well-defined areas. The broad dorsal and ventral commissures lie close together and at each end enlarge to form ganglia. The dorsal and ventral ganglia of each side fuse with one another posteriorly. The outer surface of each ganglion is rounded and grooved in such a way as to differentiate an anterior and a posterior region. The lateral nerve cords arise from the point of fusion of the dorsal and ventral ganglia on each side and extend throughout the strobila, giving off at intervals paired nerves which pass dorsally and ventrally around the proglottid just within the layer of longitudinal muscles (Fig. 16). The bothridial nerves arise one from the posterior region of each ganglion just in front of the region of the nerve cord. They extend outwards one into each peduncle where they bifurcate. The bothridial nerves could not be traced to their extremities. From the anterior region of each ganglion arises an anterior nerve which passes forwards and soon divides into three branches. The two inner branches supply the myzorhynchus while the outer extends over the anterior face of the peduncle just below the surface layers. The four ganglia and commissures contain large ganglion cells, and the brain therefore in this species, unlike some other cestodes, is the true nerve centre.

Excretory system

A dorsal and a ventral excretory vessel extend throughout the body on each side. The dorsal vessel is considerably smaller in diameter than the ventral (Fig. 16) which is most conspicuous in the immature region of the strobila. In the neck the vessels are of more uniform diameter. The arrangement in the scolex is very simple (Fig. 9), any apparent complication being due to the coiling of the vessels. The dorsal vessels pass into the peduncles of the two dorsal bothridia, and the ventral vessels pass into the peduncles of the ventral bothridia. In each case the vessels run in a coiling manner up to the distal extremity of the peduncle where each vessel turns back, the two dorsal ones turn ventrally and the two ventral ones dorsally. At the base of the peduncles they meet and the dorsal and ventral vessels of each side fuse. No ring vessel is apparent at the apex of the scolex. In the peduncles the ventral vessels are of slightly greater diameter than the dorsal and no anastomosis occurs. In the dorsal vessels, however, a certain amount of anastomosis takes place at the apex of each loop.

Genital system

The genital atrium is deep and tubular measuring 0·09 mm. in depth and 0·047 mm. in diameter (Figs. 14, 17). It lies transversely just behind the middle of the lateral margin passing dorsally to the lateral nerve cord.

Male genitalia. There are 38–40 testes arranged in two groups occupying the central

region of the proglottid. They are the first rudiments of the genital system to appear, and in the early part of the strobila are limited on either side by the very broad ventral excretory vessels. In the mature segment the testes are limited laterally by the vitellaria. They are large oval bodies measuring 0·16 × 0·072 mm. and fall into two groups, for the most part two layers deep, one on each side of the uterus (Fig. 14). They do not extend behind the ovary. The vasa efferentia unite to form an extremely long and coiled vas deferens which lies just anterior to the ovary, dorsally and more or less in the middle line (Figs. 14, 17). This part of the vas deferens is packed with spermatozoa and apparently functions as a vesicula seminalis. The cirrus sac measures 0·244 mm. in length with a maximum breadth of 0·076 mm. at its base. It lies dorsally to the vagina and a little behind it so that the two openings into the genital atrium are somewhat obliquely placed. There is no internal vesicula seminalis. The vas deferens enters the cirrus sac at its base where it forms several coils before becoming continuous with the cirrus. The cirrus is a straight, well-developed, unarmed tube which runs almost the whole length of the cirrus sac. The area between it and the wall of the sac is filled with prostate gland cells.

Female genitalia. The ovary is situated at the posterior end of the proglottid. It is bilobed in surface view (Fig. 14) and each lobe is again divided in a plane parallel to the dorsal and ventral surfaces of the body so that it appears X-shaped in transverse section (Fig. 16), and occupies the whole depth of the medullary region. The oviduct arises from the ventral side of the narrow median region of the ovary (Figs. 14, 15, 16). It passes posteriorly, and shortly after its origin it receives on its dorsal side the vagina. Behind the ovary the oviduct turns and proceeds to the dorsal side of the segment (Fig. 15). On its ventral bend it receives the median yolk duct formed by the union of a transverse yolk duct from each side. The portion of the oviduct beyond this is the ootype and is surrounded by shell glands which form a wedge-shaped mass fitting between the lobes of the ovary. The oviduct emerges from the shell gland complex dorsally and may now be called the uterine duct, which turns sharply and runs in an oblique dorso-ventral direction across the segment to open into the uterus on its postero-dorsal face (Figs. 14, 15, 16). The uterus is a median blindly ending tube which extends from the anterior extremity of the segment to just in front of the median portion of the ovary. In the mature segment it is slightly lobed. No gravid segments were found. The yolk glands are situated laterally forming a broad band on each side of the segment extending along its whole length between the testes and nerve cords (Figs. 14, 16). The terminal portion of the vagina runs more or less parallel to the cirrus sac and is somewhat longer than it (Fig. 17), its walls consisting of a layer of cells. Having reached nearly to the centre of the segment the vagina turns posteriorly, emerging from among the coils of the vas deferens and, turning ventrally, passes posteriorly to the median part of the ovary, between it and the shell glands, to open into the oviduct (Figs. 14, 15). The vagina and uterine duct therefore cross one another (Fig. 15). As no gravid segments were available the eggs could not be examined.

From an examination of the anatomy it can be seen that *Anthobothrium auriculatum* (Rud.) is a distinct species not synonymous with any other species of the same genus or of a related genus. Its chief characteristics are seen in the dimensions of the various parts of the body, the position of the genital pores, and the auriculate bothridia. The myzorhynchus, too, is a distinctive feature. In the contracted condition the scolex bears

a striking resemblance to that of *Anthobothrium dipsadomorphi* (Shipley, 1900) from the intestine of a 'Malagea' snake *Dipsadomorphus irregularis* caught on New Britain. It is, however, highly improbable that the two forms are synonymous, the one occurring in a fish in the Atlantic and the other in a snake on an island in the Pacific.

List of abbreviations. *a.* apex of bothridium; *a.m.* adjacent muscles; *a.n.* anterior nerve; *a.r.* anterior region of ganglion; *b.* bothridium; *b.n.* bothridial nerve; *br.* brain; *c.* commissure; *c.m.* circular muscles; *c.s.* cirrus sac; *c.s.m.* cirrus sac muscles; *cu.* cuticular frill; *d.* dorsal; *d.e.v.* dorsal excretory vessel; *d.l.m.* deep longitudinal muscles; *e.v.* excretory vessel; *f.* floor of bothridial funnel; *g.a.* genital aperture; *g.c.* ganglion cell; *i.m.r.* inner muscular ridge; *l.* loculus; *l.my.m.* longitudinal muscles of myzorhynchus; *m.l.* muscles separating successive loculi; *my.* myzorhynchus; *n.c.* nerve cord; *o.m.* oblique muscles; *o.m.r.* outer muscular ridge; *oot.* ootype; *ov.* ovary; *p.* peduncle of bothridium; *p.r.* posterior region of ganglion; *r.d.g.* right dorsal ganglion; *s.* sucker; *sh.g.* shell glands; *sl.f.* semilunar fold; *t.* testis; *t.m.* transverse muscles; *ut.* uterus; *ut.d.* uterine duct; *v.* ventral; *v.d.* vitelline duct; *v.def.* vas deferens; *v.e.v.* ventral excretory vessel; *v.m.* vaginal muscles; *vag.* vagina; *vit.* vitellaria.

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THE RELATIONSHIP BETWEEN MALLOPHAGA AND HIPPOBOSCID FLIES

By THERESA CLAY and COLONEL R. MEINERTZHAGEN

(With 2 Figures in the Text)

It has been known for a long time that certain species of Mallophaga attach themselves to hippoboscid flies, the act taking place on the bird host. This has been referred to as Phoresy, 'a type of interrelationship between insects in which one is carried on the body of another larger insect, but the former does not feed on the latter', or, in other words, free passage without food.

The recorded cases are as follows:

1857. Aube. Two Mallophaga, said to be those from a magpie, *Pica pica*, recorded from *Ornithomyia aviculare* L. (quoted by Thompson, 1934).

1890. Sharp. Records a single *Ornithomyia aviculare* from Dartford, Kent, 'to which several specimens of Mallophaga were firmly adhering, apparently by the mandibles'.

1910. Mjöberg. Records two *Ornithomyia aviculare* from a starling (*Sturnus v. vulgaris*) in Sweden, the one with seven and the other with three *Philopterus leontodon* adhering to the long hairs of the abdomen. (*P. leontodon* = *P. sturni*.)

1910. Wanach. Records a *Philopterus* sp. probably from *Turdus m. merula*, the blackbird, on the abdomen of an *Ornithomyia aviculare* near Berlin.

1911. Jacobson. Records a single *Ornitoeca pusilla* taken off a pitta (*Eucichla cyanura*) near Batavia in Java with a Mallophaga clasped between the legs of the (dead) fly.

1912. Forsius. Records a single *Ornithomyia aviculare* with two *Degeeriella quadrulata* adhering to the base of the wing of a blackcock, *Lyrurus tetrix* in Finland. (*Degeeriella quadrulata* = *Lagopoecus lyrurus* Clay.)

Also a single *Ornithomyia aviculare* with two *Degeeriella uncinosa*, adhering, one to the hind tibia and another to the abdominal hairs. (*D. uncinosa* = *Bruelia uncinosa*.) Host *Corvus corone cornix*, the hooded crow.

1920. Banks. Records an *Ornithomyia* to which two Mallophaga were attached, one on each side near the tip of the abdomen.

1922. McAtee. Records an *Ornithomyia aviculare* from Saskatchewan on 11 August 1920, to which was attached a *Degeeriella rotundata*. Host unknown. A second *Ornithomyia aviculare* from Oregon on 30 September 1920 had a second *Degeeriella rotundata*, host *Corvus brachyrhynchus hesperis*, an American crow. (*Degeeriella rotundata* = *Bruelia rotundata*.) In both cases the Mallophaga were attached by their mandibles to the upper surface of the abdomen near the hind margin.

1922. Johnson. Records the same specimen as Banks. Two specimens of undetermined Mallophaga were attached to a single *Ornithomyia auchineuria* taken from a jay, *Perisoreus canadensis barbouri*, on Anticosti Island on 3 September 1919. The Mallophaga were one on each side of the abdomen at posterior edge of 1st segment.

1927. EWING. Records a specimen of *Ornithomyia aviculare* from a song sparrow, *Melospiza m. melodia*, to which were attached two *Degeeriella interposita* (=*Bruelia interposita*). They were adhering to the body wall of abdomen by the mandibles. In a second case, a specimen of *Ornithomyia aviculare* from a catbird, *Dumetella carolinensis*, to which was attached a single *Bruelia interposita*. In both cases the specimens were taken in Ohio.

1928. WARBURTON. Records a specimen of *Ornithomyia aviculare* captured on a window in Cambridge (England). Attached to the hairs of the abdomen was a specimen of *Degeeriella marginalis* (=*Bruelia marginalis*) a common parasite on members of the genus *Turdus*.

1928. SPENCER. Records a single *Ornithomyia aviculare* taken on a Steller's jay, *Cyanocitta s. stelleri*, on Vancouver Island, and to it were attached sixteen *Degeeriella deficiens* (=*Bruelia deficiens*) holding on to the abdominal tergites with their mandibles.

1933. THOMPSON. Records an *Ornithomyia aviculare* taken in Hertfordshire from a young song thrush, *Turdus philomelos clarkei*, to which were attached three *Bruelia marginalis*. They were adhering to the posterior margin of the abdomen.

A second specimen of *Ornithomyia aviculare* found in the British Museum collection had eleven *Bruelia marginalis* fixed to the posterior portion of the abdomen. It was caught on a window at Woking in Surrey.

1934. THOMPSON. Records (ex Waterston) two specimens of *Ornithomyia aviculare* from the Shetlands each with a *Philopterus sturni* attached. Also (ex Britten) a specimen of *Ornithomyia aviculare* found on a window in Cumberland with a *Bruelia marginalis* attached.

1935. THOMPSON. Records a specimen of *Lynchia* sp. taken from an African weaver, *Euplectes orix sundevalli*, with a Mallophaga attached to abdomen and a specimen of *Ornithomyia chloropus* taken from a fieldfare, *Turdus pilaris*, in Sweden with a single *Bruelia marginalis* attached.

It is relevant to record here the case of *Trichodectes tibialis* being found attached to Culicidae (Thompson (1933) (ex Peus, *Z. Parasit.* **5**, 740–41).)

It is also relevant to mention the case of mammal Mallophaga (*Gyropus* and *Trichodectes*) found attached to a dragonfly (*Ischnogomphus jessei* Williamson) in Columbia. (Mann (1920).)

In addition to the above, the following cases have come to our notice:

1. *Garrulus glandarius rufitergum*. Jay, Berkshire, July 1941. Specimen wrapped up and immersed in chloroform fumes at once. Host was infested with six *Ornithomyia avicularis* on two of which adhered Mallophaga. On one were 2♀ *Bruelia glandarii* attached to the lower abdomen; on the other was a single ♀ *Bruelia glandarii* on the left lower flank. Total population on host, 9 ♂, 26 ♀, 8 im. *Bruelia glandarii*. (Slide 14458, Meinertzhagen coll.)

2. *Aphelocoma c. californica*, California jay, California, no date. Specimen received from Bequaert. 1 ♀ *Bruelia* (probably from a species of Corvidae, but not from *Aphelocoma*) on *Ornithoica confluenta*, attached to the vein of the wing. One mandible

of *Bruelia* is underneath the junction of the costa and first longitudinal vein, pressing it upwards against the other mandible which has pierced the wing and lies on top (see Fig. 1). (Slide, Meinertzhagen coll.)

3. *Pastor roseus*, rose-coloured Pastor, Deccan, India, February 1937. Collected by Meinertzhagen. 1 ♀ *Philopterus* on *Ornithoica metallica*, attached to the last segment of the abdomen, probably by gripping the base of the hairs. Total population on host: 2 ♂, 3 ♀, 1 im. *Philopterus*; 1 ♂, 2 ♀, 1 im. *Bruelia*. (Slide 8828, Meinertzhagen coll.)

4. *Sturnus v. vulgaris*, starling, Estonia, August 1934. Collected by Meinertzhagen. 1 ♀ *Bruelia* on *Ornithomyia lagopodis*, attached to the last segment of the abdomen. Total population on host: 1 ♂ *Bruelia* and 5 *Myrsidea*. (Slide 1434, Meinertzhagen coll.)

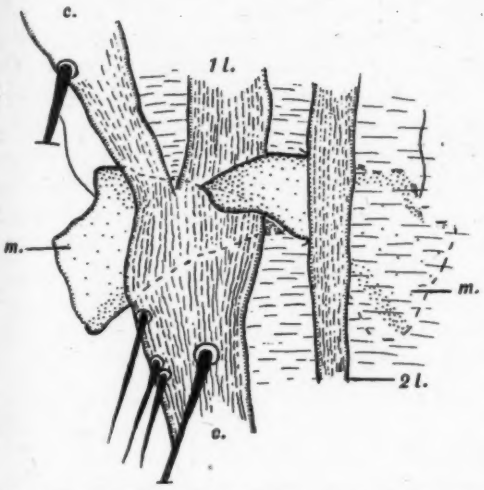

Fig. 1. Portion of the wing of *Ornithoica confluenta*, showing mandibles (*m*) of *Bruelia*. *c*, costa; *1l* and *2l*, 1st and 2nd longitudinal veins.

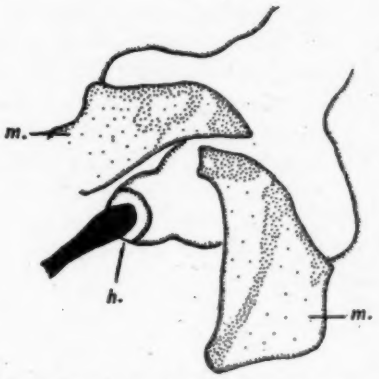

Fig. 2. Posterior end of the abdomen of *Ornithomyia avicularis* with mandibles (*m*) of *Bruelia merulensis* attached to a hair (*h*).

5. *Sturnus vulgarus zetlandicus*, Shetland starling, Orkneys, August 1938. Collected by Meinertzhagen. A single *Ornithomyia lagopodis* was caught on bird when shot and found to be free of Mallophaga. Insect returned to host for an hour and then host was chloroformed. The dead fly was then found to have 3 ♀ *Philopterus sturni* attached to abdomen. Total host population: 9 ♂, 13 ♀, 3 im. *Philopterus sturni* and 5 ♂, 25 ♀ *Bruelia*. (Slide 11479, Meinertzhagen coll.)

6. *Sturnus vulgaris zetlandicus*, Shetland starling, Orkneys, August 1938. Collected by Meinertzhagen. A single *Ornithomyia lagopodis* was caught on bird when shot and found to be free of Mallophaga. Insect returned to host for an hour and then host was chloroformed. The dead fly was found to have 7 ♂ and 21 ♀ *Philopterus sturni* attached to abdomen. Total host population: 24 ♂, 32 ♀, 21 im. *Philopterus sturni* and 3 ♂, 24 ♀, 9 im. *Bruelia*. (Slide 11525, Meinertzhagen coll.)

7. *Sturnus vulgaris zetlandicus*, Shetland starling, Orkneys, August 1938. Bird chloroformed within an hour of death. On shaking out for parasites, a single *Ornithomyia lagopodis* was found to have 2 ♂, and 4 ♀ *Philopterus sturni* attached, two on one flank of the abdomen and four on the posterior end of the abdomen. Total host population: 15 ♂, 24 ♀, 5 im. *Philopterus sturni*, 6 ♂, 2 ♀, 4 im. *Bruelia* and 2 ♀ *Menacanthus*. (Slide 11413, Meinertzhagen coll.)

8. *Sturnus vulgaris zetlandicus*, Shetland starling, Orkneys, August 1938. This is perhaps the most remarkable of all cases which have come to our notice and deserves recording in detail. Immediately after being shot the bird was examined and seven *Philopterus* were seen to be adhering to the inside of the webs of some of the left wing feathers. On the right wing were eight *Philopterus* adhering to feathers. That makes fifteen *Philopterus* in all. The specimen was wrapped up in muslin at once and after about two hours was immersed in the fumes of chloroform. When shaken out for parasites, a hippoboscid fly (*Ornithomyia lagopodis*) fell out. 1 ♂ and 6 ♀ *Philopterus sturni* were found to be adhering to the abdomen, 3 ♀ *Philopterus sturni* were still adhering to the wing and 3 ♂ and 2 ♀ were shaken from the body. The whole philopterid population were therefore accounted for, some of which had taken the precaution of boarding the fly as the host cooled off, in other words, the Mallophaga appeared to use the fly as a lifeboat. Total host population: 4 ♂, 11 ♀ *Philopterus sturni* and 7 ♂, 25 ♀ *Bruelia*. (Slide 11308, Meinertzhagen coll.)

9. *Sturnus vulgaris zetlandicus*, Shetland starling, Shetland, August 1939. Collected by Meinertzhagen. 1 ♀ *Philopterus sturni* on *Ornithomyia lagopodis* attached to the last segment of the abdomen. This fly was caught on the window and placed on the dead bird soon after it was shot. After chloroforming, the dead fly had the *Philopterus* attached. Total host population: 1 ♂, 4 ♀ *Philopterus sturni*, 3 ♂, 8 ♀ *Bruelia*, and 1 ♀ *Myrsidea*. (Slide 13609, Meinertzhagen coll.)

10. *Pipilo maculatus megalonyx*, Towhee (U.S.A.). Received from Bequaert. 1 ♀ *Bruelia* on *Ornithomyia confluenta*, attached to the vein of the wing. The species of *Bruelia* is probably from some member of the Corvidae. (Slide, Meinertzhagen coll.)

11. *Tschagra s. senegallus*, bush shrike, Morocco, October 1938. Collected by Meinertzhagen. 2 ♀ *Bruelia* on an unidentified hippoboscid fly, one attached to each flank of the abdomen. The species of *Bruelia* is the same as occurred on the host. Total host population: 1 ♀ *Philopterus*, 6 ♂, 7 ♀, 2 im. *Bruelia*. (Slide 11946, Meinertzhagen coll.)

12. *Turdus m. migratorius*, the American robin, Mass., U.S.A. Received from Bequaert. 2 ♀ *Philopterus* on *Ornithomyia fringillaria*, one attached to each side of the abdomen. (Slide, Meinertzhagen coll.)

13. *Cuculus c. canorus*, cuckoo, Suffolk, August 1935. 1 ♀ *Bruelia merulensis* on *Ornithomyia avicularis* attached to the hairs on the posterior end of the abdomen. *Bruelia merulensis* is only known from *Turdus merula*, the blackbird. There were no other Mallophaga on the cuckoo which was a juvenile specimen. See Fig. 2. (Slide 3919, Meinertzhagen coll.)

Of these thirteen cases, ten were collected by ourselves, and it is remarkable that between 200 and 300 hippoboscid flies have been taken from freshly killed birds in four continents with such meagre results.

The following additional experiments were carried out with hippoboscid flies in the Orkneys and Shetlands in August 1938 and August 1939. Eight living hippoboscids (*Ornithomyia lagopodis*) were placed on eight freshly killed and warm starlings known to be infested with *Bruelia* and *Philopterus* and remained in contact with the birds for two hours without a single fly having a Mallophaga attached. Also, four hippoboscids of the same species, fresh but dead, were placed on freshly killed starlings known to be infested with *Philopterus* and *Bruelia* without any result after three hours.

In addition, six living *Philopterus* and eight living *Bruelia* from a starling were placed in a small glass phial with two living hippoboscids (*Ornithomyia lagopodis*) for two days without any resultant attachments, though both classes of insects were in continual contact.

To revert for a moment to cuckoos. A recently fledged cuckoo, a beautiful albino now in the British Museum, was picked up dead in the New Forest on 18 July 1939. We saw it in the British Museum on the following day. It was then infested with 1 ♀ *Bruelia merulensis* and 2 *Philopterus* sp., probably from *Delichon urbica*, the house martin.

Young cuckoos are reared by foster parents and have no contact with their own parents; in fact, adult cuckoos leave Britain before their offspring are fully fledged. Therefore any Mallophaga found on a young cuckoo must have come either from the foster parent or from an infested hippoboscid fly. It is interesting to note that neither the blackbird nor the house martin are foster parents to the cuckoo, except in cases of negligible value.

In addition to the above case we have examined five young cuckoos in Britain and Estonia in July. None had Mallophaga. One had nine, two had five, one had two and one had no hippoboscid flies. In only one case were Mallophaga attached to the fly (see case 12 above). But it is clear that hippoboscid flies are partial to young cuckoos.

Of seven adult cuckoos shot in Britain, Poland and Afghanistan in summer, none had hippoboscid flies on them, but every specimen was fairly heavily infested with Mallophaga.

Of nine cuckoos obtained in Ushant on spring migration in 1935, there were two females. One of these had bred in the previous year and she was infested with three species of Mallophaga. The other female was a bird of the previous year and had never bred. She had a single *Cuculoecus* which must have been carried by some agency other than contact. The fact that she had but a single parasite indicates carriage by hippoboscid fly during the winter in tropical Africa.

It is difficult and unproductive to generalize on all the above evidence, which is insufficient and fragmentary. All we can say is that the only genera of Mallophaga known to be carried by hippoboscid flies are *Philopterus* and *Bruelia*, and that these probably attach themselves to the roots of the hairs or veins of wings and do not embed their mandibles into the abdomen of the fly. It is also significant that Mallophaga attach themselves to flies after the death of the host.

Any further evidence on this subject will be welcomed by the authors. Isolated cases, if published as they occur in various journals, are apt to be overlooked. If collected by one agency they could be collated and published periodically in co-ordinated form.

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Since going to press the following additional record has come to notice:

Emberiza c. citrinella, yellow hammer, Devon, October 1942. 2 ♀ *Bruelia* sp. on *Ornithomyia fringillina*, collected by Meinertzhagen, the Mallophaga being attached to the upper surface of the abdomen. There were no other Mallophaga on the host. (Slide 14802, Meinertzhagen coll.)

THE INCIDENCE OF LARVAL TREMATODES IN MALES AND FEMALES OF THE GASTROPOD *LITTORINA NERITOIDES* (L.) ON THE PLYMOUTH BREAKWATER

By AVERIL M. LYSAGHT, Ph.D.

(With 1 Figure in the Text)

In the course of my work on *Littorina neritoides* (L.) I found that this mollusc was parasitized by four larval trematodes. The two most common species were a metacercaria (Metacercaria A) and parthenitae and cercariae of a species (Cercaria B) in the Ubiquita group (Lysaght, 1941). The snail acted as secondary and primary intermediate host, respectively, to these two trematodes whose life histories are unknown. The Hon. Miriam Rothschild, who kindly read and criticized my paper in manuscript, was much interested in this type of parasitism, as it suggested a useful comparison for her work on *Peringia ulvae*, in which species the incidence of trematode parasites appears to have a definite relation to the size of the host (A. & M. Rothschild, 1939); and at my suggestion she agreed to make use of my data in a separate paper (Rothschild, 1941). Unfortunately, I was absent in New Zealand at the time, and, owing to the slowness of communications in wartime, we were unable to discuss adequately some of the points that arose. It is therefore necessary to amplify now some of my data which throw a rather different light on some of her conclusions.

I am much indebted to Prof. Ritchie for allowing me to use the Library in the Zoological Department of Edinburgh University, to Dr A. C. Aitken who has very kindly read and criticized the two papers in question, and to my fellow-zoologists for much helpful discussion on most of the points involved.

It seems best to begin by quoting the summary from Rothschild (1941): 'If the number of infections with (*a*) trematode parthenitae and cercariae using *Littorina neritoides* as first intermediate host only, and (*b*) encysted metacercariae using *L. neritoides* as second intermediate host only, are plotted against the size of the snails, two different curves result. The first shows a low rate of infection in the small size groups, but a steep upward slope rising to 91% in the large size groups. The second shows a curve increasing uniformly to 87% infection.

'Possible interpretations are discussed, and it is concluded that the difference is probably due to the fact that primary infections cause accelerated growth in the host.'

The first point that arises here is that the graph showing the relationship between size and infection (Rothschild, 1941, Fig. 1) is obscure. It shows as comparable, curves of the total percentage infections with Metacercaria A and Cercaria B for the whole population of snails, and, on the same set of ordinates, the percentage infections with either trematode in that fraction of the population left after the numbers of snails infected with the other trematode have been subtracted. This is briefly referred to, without comment, four pages farther on. Also in some cases the values of the points have been

slightly increased by the addition instead of the subtraction of the percentage infection by a third species of trematode.*

If the infections with either Metacercaria A or Cercaria B are plotted as percentages of the whole population the curves present a different trend, and these percentages are therefore plotted below (Fig. 1). The curve for Metacercaria A without Cercaria B now rises fairly smoothly to 52% in snails of 6·5 mm., and then drops sharply. The curve for Cercaria B alone shows a consistently low rate of infection and fluctuates about values of 5 and 10%. Values for total infection with Cercaria B, that is, including the cases in which both trematodes infect the same snail, however, rise sharply from the 6 mm. size group, that is, at approximately the same time as infections of Metacercaria A drop off.

Rothschild (1941) suggests that the percentage infection with Metacercaria A can be taken as an estimate of the growth rate of the snails. The metacercariae do not appear to exert any physiological influence on the snails, and where *total* infections are concerned they appear to increase proportionately with the age of the snail. She points out that the curve for Cercaria B differs from that for Metacercaria A and 'is fundamentally the same as that demonstrated for *Peringia ulvae* infected with larval trematodes'. She has shown that when snails of this species were infected and kept under laboratory conditions, they grew faster than uninfected ones and ultimately attained a greater size (A. & M. Rothschild, 1939). Total infections of Cercaria B show values supporting her statement, but if the dissimilarity in the curves for both trematodes is due to growth stimulation by Cercaria B, as she suspects, the percentage infections with this species alone should also increase in the larger snails; this, however, does not occur. She goes on to say (1941, p. 71): 'Moreover, assuming that infection occurs at random, and increases proportionately with the age of the snail a far more probable computed growth curve is obtained if it is based on the curve shown for percentage infection of Metacercaria A.'

This assumption of random infection is the keystone of Mr Spooner's computations on the growth rate of *Littorina neritoides*. He says (in Rothschild, 1941, p. 72): 'It is permissible to assume that the average rate of infection of each trematode remains constant or at least is independent of the size of the snail', and further on, 'If no other factor affects the original percentage infection curves than the most straightforward conditions which have been assumed, the two growth curves should be coincident.' He concludes: 'That it is the curves derived from the data on Cercaria B which are anomalous: there is clearly an undue concentration of snails infected with this cercaria among the larger size groups.... The results obtained from them (single infections) are in entire agreement with those given by the total infection data.'

It seems to me that the assumption of random infection cannot be justified at present as the life histories of the trematodes concerned are unknown, and we do not know which invertebrate is the primary intermediate host of Metacercaria A. No other snails except an occasional *L. rudis* were collected by me in the potholes of the Plymouth Breakwater, from which most of the material for my original paper was taken. It has been suggested that a large limpet may be the primary host. It is abundant on the slopes of the breakwater, but I have made no estimate of its density. Often on calm

* This third trematode, Cercaria C, infected 2·23 and 2·81%, respectively, of the male and female snails examined (Lysaght, 1941), but as it does not appear to cause sterility in the host or to show any marked preference for either sex the comparatively few cases in which it is present have been included in the whole population. Thus the phrases 'Metacercaria A alone' or 'Cercaria B alone' refer to the absence of one or the other of these two larval trematodes only.

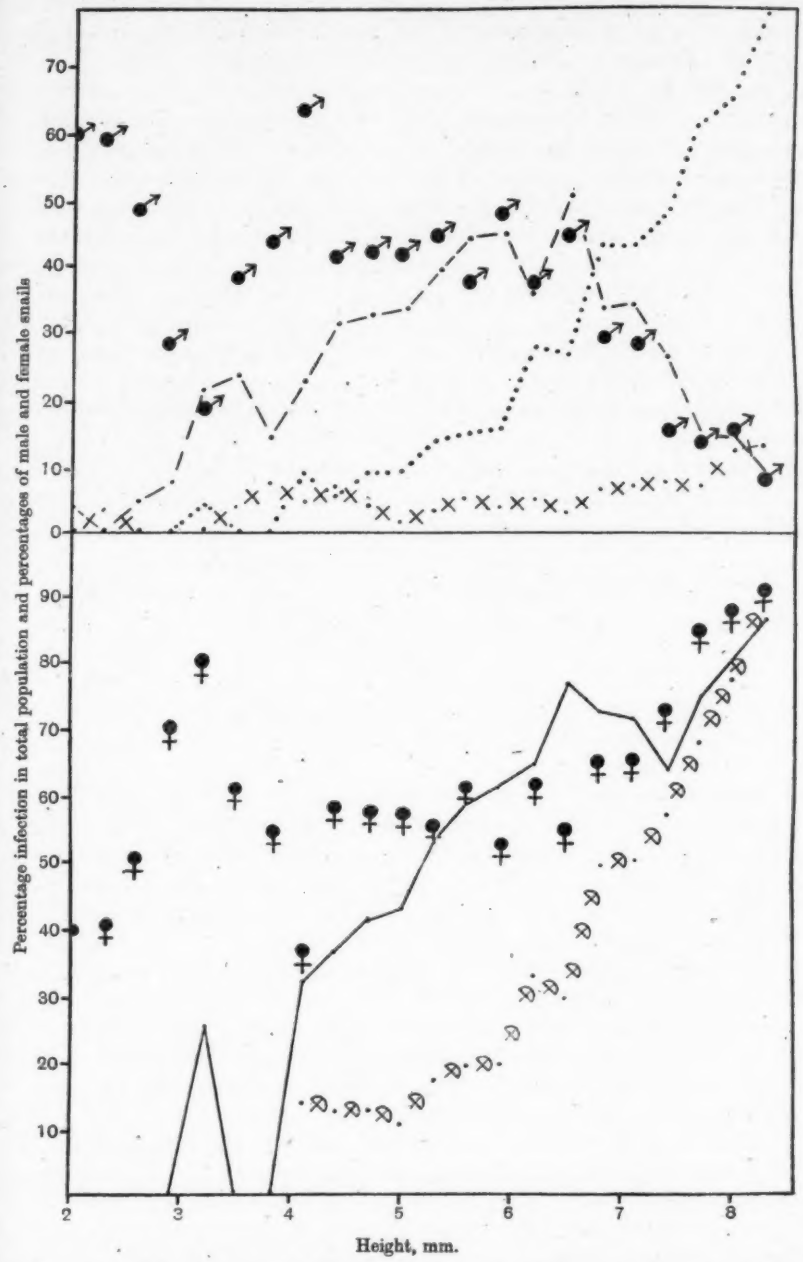

Fig. 1. Trematode infections in total snail population. Broken line, Metacercaria A alone; dotted line, Metacercaria A with Cercaria B; solid line, Metacercaria A plus (Metacercaria A plus Cercaria B); single crosses Cercaria B alone; crosses combined with semicircle, Cercaria B plus (Cercaria B plus Metacercaria A).

days, while working on a falling tide, I have been aware of the murmur caused by the rasping of the limpets' radulae as they browsed along the rocky slopes, and they are sufficiently abundant for the citizens of Plymouth to collect them for food.

In dealing with the distribution of *L. neritoides* on the breakwater I showed that the smallest snails inhabited the lowest part of the zone (Lysaght, 1941, Table 1, Figs. 2–3), and this coincides with the upper part of the limpet zone. If the limpets should prove to be the primary intermediate host of Metacercaria A, *L. neritoides* would perhaps be attacked at a very early stage after metamorphosis, and long before the snails have migrated to the potholes. The young snails are more heavily infected with the metacercariae than with Cercaria B. If the miracidia giving rise to the latter hatch from eggs present in the numerous bird droppings on the top of the breakwater they are more likely to attack the older snails already in the potholes than the younger ones on the slopes. Even if there are no free-living miracidia and the trematode eggs are thus ingested by the snails it seems unlikely that the smaller snails in the more exposed habitat are as liable to be infected as the larger snails on top. In any of these possible cases random infection could scarcely be said to occur.

Another explanation of at least part of the differences between the curves shown in Fig. 1 is to be found, as Miss N. G. Sproston has suggested to me, in the different frequency of infection of male and female snails (Table 1).

Table 1. *Percentage infection of males and females of* Littorina neritoides *by Metacercaria A and Cercaria B*

	Males	Females
A plus (A plus B)	60·35	52·7
A alone	47·6	28·7
(A plus B)	12·75	24·0
B alone	1·8	5·7
B plus (A plus B)	14·65	29·7

These differences in the percentage infection are fairly constant, but less so in the case of Metacercaria A than Cercaria B (Lysaght, 1941, Fig. 11). In this paper it was pointed out that the percentage of males in the population was significantly lower in the larger size groups (Fig. 2). Now, Metacercaria A, alone, infects 47·6% males and 28·7% females. Where Metacercaria A occurs with Cercaria B, however, only 12·75% males are attacked compared with 24% females. So that the presence of Cercaria B appears to modify the apparent preference of the metacercariae for the male snails. Since this is so it is to be expected that in the smaller size groups of snails where the males are more numerous infections with Metacercaria A, alone, should increase to a certain point, and that in the larger size groups where the numbers of male snails fall off, these infections should also fall off, and that, at the same time, the proportion of female snails infected with both trematodes should increase.

The percentage infections in the whole population, and the percentages of male and female snails are all plotted in Fig. 1, and it will be seen that there is a close connexion between the decrease in the number of males and the percentage infections with Metacercaria A alone in the higher size groups, while the infections with both trematodes rise with the increase with the numbers of females. It has been suggested that sex reversal may cause the decrease in the number of males among the larger snails, but this decrease occurs in four species of the genus *Littorina*, also in a species of *Vivipara*. Sewell

(1924), discussing growth rate in *Littorina scabra* L., shows that the females grow faster than the males. He says 'There is a marked disparity in the size of the sexes', and this is clearly shown by the measurements he gives of 66, 73 and 21 snails, in their second, third and fourth years, respectively. Further, he says: 'Examples that were in their second year in 1921 were in their third year in 1922, and it is extremely interesting to note the way in which the number of males becomes reduced in proportion to the number of females. I have shown that an exactly similar state of affairs is found in *Vivipara bengalensis* and it is probably of universal occurrence among Mollusca in the tropical regions. During the period of life between the third and fourth year this disparity in the proportion of the sexes becomes even more marked....'

The same differences are present in *Littorina obesa*: 'we again find, as in *Vivipara bengalensis* and *Littorina scabra*, a tendency for the proportions between the sexes to vary as age progresses; thus:

	Males	Females
In the second year of life the proportion is	52	48
In the third year of life the proportion is	27	73'

Moore (1937), referring to *L. littorea*, says: 'Excepting the first month when the amount of growth was so small as to be difficult to measure, and therefore not very reliable, there is in all cases a definitely greater rate of growth in the females than in the males....Such a differential growth rate explains the preponderance of females over males found in the larger sizes. Pelseneer (1926), in an examination of 516 individuals of from 13 to 15 mm. in height, found 50·96% females, as compared with 67·18% females in a sample of 192 individuals over 2·2 cm. in height. Table 11 shows a similar condition at Trevol, the males and females being present in about equal proportions up to a height of 25 mm., after which the proportion of females rises rapidly to three-quarters of the population.'

Table 2

Height in mm.	No. of males	Percentage of population	Height in mm.	No. of males	Percentage of population
4·7	3	27·3	6·2	16	23·1
5·0	2	6·5	6·5	30	29·15
5·3	15	29·4	6·8	23	27·66
5·6	17	23·46	7·1	15	26·3
5·9	24	25·4	7·4	13	31·3

As the males in *L. neritoides* are also less numerous in the larger sizes it seems reasonable to suppose that in this species, too, there is a definitely greater rate of growth in the females. I found no evidence of sex reversal and the probability that it does not occur is also supported by the fact that the percentage of males in the population is almost the same in unparasitized snails as in the whole population (Lysaght, 1941, Fig. 8). Also, if only the snails in which Cercaria B occurs (both alone and with Metacercaria A) are considered, the percentage of males is comparatively stable (Table 2), and certainly does not show any sudden decrease in the larger sizes such as would be expected if the decline in the total male population (Fig. 1) were due to sex reversal caused by Cercaria B.

Rothschild, referring to the accumulation of specimens infected with trematode larvae (parthenitae and cercariae) among large snails, says in a footnote (1941, p. 75): 'It is of interest to note that in localities where Cercariae B and C were not found in *Littorina neritoides*, the largest snails (with one exception) did not exceed 6 mm. in height.' The

largest snails found infected with these trematodes in localities other than the breakwater did not, however, exceed 7·2 mm. in height, while on the breakwater the largest snail found was 10·4 mm., and specimens of 8 and 9 mm. were not very uncommon. It should be noted that in no other locality examined were conditions as favourable for shelter and continuous feeding as on the breakwater. In discussing factors which might lead to a high rate of infection in large snails she mentions the decrease in growth rate with increasing age shown by Moore (1937) in *L. littorea*, and by myself in *L. neritoides*. My data (1941, Table 4) suggest that the snails on the breakwater may take some decades to reach their maximum height, and this comparatively great age combined with the peculiar environment would greatly increase the chances of infection.

Summary

Females of *Littorina obesa*, *L. scabra* and *L. littorea* have been shown by other workers to grow more rapidly than the males so that they predominate in the larger size groups. They are significantly more numerous than the males among the larger specimens of *L. neritoides* on the Plymouth Breakwater.

More male than female snails are infected by a larval trematode, Metacercaria A, when it occurs alone, and the percentage infection falls when the proportion of males falls. A second larval trematode, Cercaria B, infects more female snails than males. Infections with this species alone remain consistently low, but where it occurs in the same snails as Metacercaria A the percentage infection rises rapidly, that is, in the larger size groups of the snails where the females predominate. Females infected by Cercaria B appear then to be attractive to the metacercariae.

Evidence is given to show that it is extremely unlikely that these large female snails were originally males in which sex reversal has occurred.

This different intensity of infection of the sexes of *L. neritoides* is considered to be primarily responsible for the shapes of the curves when infection is plotted against size, and it does not appear likely that primary infections with larval trematodes cause acceleration of the growth rate in this species.

It is thought that ecological factors on the breakwater are likely to be the chief causes of the large size attained there by *L. neritoides*.

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CASES OF ABNORMAL DEVELOPMENT IN THE ARGASID TICK, *ORNITHODORUS MOUBATA*

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(With 3 Figures in the Text)

1. Partial twinning

During the course of experiments entailing the examination of about 8000 individuals of this tick, two cases of partial twinning were noticed. The condition was seen in the posterior half of a fifth stage and a third stage nymph, which later moulted to become a female and male respectively.

The twinned region was almost identical in the two ticks and that of the female is shown in Fig. 1. The body behind the preanal groove (*p.g.*) was considerably wider than in a normal tick (Fig. 3A), whereas in front of this groove the width was normal. The anus (*r.a.*) with the paired anal disks (*a.d.*) was duplicated, and there was almost complete twinning of the marginal discal areas except in the region of a larger central area

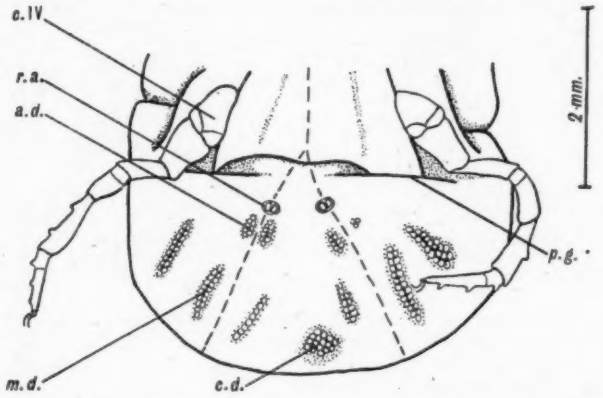

Fig. 1. Ventral aspect of the posterior region of a partially twinned *Ornithodorus moubata*. The broken line marks the physiological median line of the organism. *a.d.* anal discal area; *c.d.* central marginal discal area; *c.* IV coxa of fourth leg; *m.d.* marginal discal area; *p.g.* pre-anal groove; *r.a.* right anus.

(*c.d.*) which represented an incomplete separation of the remaining two discal areas. Thus there were only seven marginal discal furrows instead of the full duplicate of the normal four. The disks mark the insertion of muscles on the inner side of the cuticle (Robinson & Davidson, 1913). The rectal sac, visible by virtue of the transparent integument, could be seen to be much larger than usual, but it was not separated into two. Both anal apertures were proved to be capable of function, but the tick was not seen to use both simultaneously. Twinning on the dorsal surface was indicated solely by duplication of discal areas, and was not so noticeable as that on the ventral surface.

Being anterior to the preanal groove the genital aperture was normal and unpaired, and the specimens were successfully mated to normal ticks, and proved normally fertile.

Certain abnormalities were noticed in the internal anatomy of the partial twins. In a normal female the single, median ovary is served by a pair of oviducts. In the twin there were two ovaries each placed laterally, but each had only one oviduct. Also, the rectal sac, though in the posterior part of the body, was only partially twinned (Fig. 2B). The right sac was perfect and into it led two malpighian tubules and the rectum as in a normal tick. Joined to the right was the left sac which had only one malpighian tubule and no rectal connexion with the gut. In place of the latter connexion there was a vesicle approximately the size of a mature egg. Each rectal sac had a functional anus. It is remarkable that the rectum connecting the right sac with the gut was not a solid strand as in a normal tick, but a hollow tube capable of giving passage to the gut contents which thus could reach the exterior by way of the rectal sac and anus. The faeces were

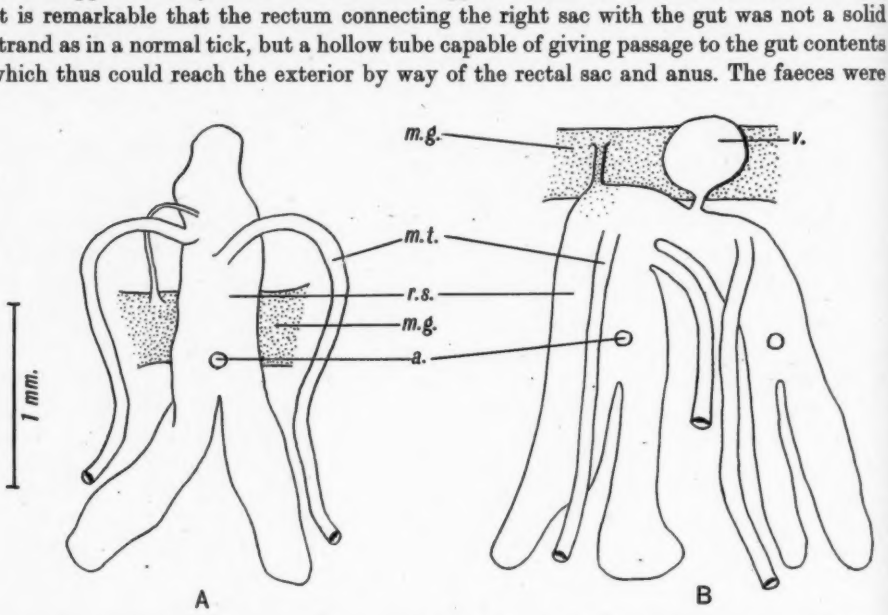

Fig. 2. Ventral view of the rectal sac of a normal *Ornithodorus moubata* (A) and that of a partial twin (B). In the partial twin the perfect bladder had two malpighian tubules and a tubular rectum joining it to the midgut. The imperfect duplicate had only one malpighian tubule and no direct connexion with the midgut. Both anal apertures were functional. *a.* anus; *m.g.* midgut; *m.t.* malpighian tubule; *r.s.* rectal sac; *v.* vesicle.

consequently tinged purplish and lacked the normal cream colour of the contents of the malpighian tubes. No abnormalities were noticed in the ventral tracheal system.

In the case of the male partial twin, the testis was split into two like the ovary of the female specimen. The bladder was also very similar with three malpighian tubules and two functional anal apertures. The rectum, however, was of normal size and occluded.

In ixodid ticks, partial twinning has been noticed by Warburton & Nuttall (1909) who described the condition in *Boöphilus decoloratus* ♂ and *Rhipicephalus sanguineus* ♂; Nuttall (1914) saw it in *R. appendiculatus* ♂, Senevet (1922) in *Hyalomma aegyptium* ♀, and Brumpt (1934) in *Ixodes ricinus* nymph, *I. hexagonus* ♀, *Rhipicephalus bursa* nymph and *Amblyomma dissimile* ♂. Except for the latter tick, which was one of a batch of sixty-seven, the recorded frequencies of 1 in 2000–3000 of this type of abnormality in the ixodids is of the same order as in *Ornithodorus moubata* (1 in 4000).

The cause of partial twinning includes physical or chemical interference with the formation of the germ band of the embryo (Huxley & De Beer, 1934; Wigglesworth, 1939) with consequent dichotomy of the proliferating region. Possible causes of the present cases are undue mechanical pressure of adjacent eggs in the batch, and a drop in temperature due to faulty incubation.

2. AN ABNORMAL MALE

A third stage nymph was noticed with a peculiar humped appearance. It fed normally and later moulted to become a male. The 'hump' (Fig. 3B) was covered with evenly mammillated cuticle and had no discal areas. On examination it was seen to be an enlargement of what would normally be the postanal region, but the anus was displaced posteriorly to the apex of the hump (Fig. 3B). Those discal areas of the cuticle which

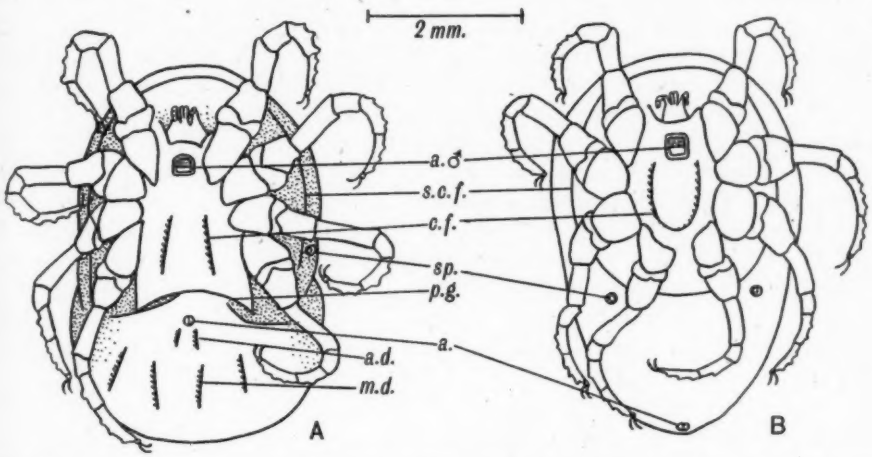

Fig. 3. Ventral aspect of normal male *Ornithodorus moubata* (A) and an abnormal male (B), in which a hump is developed in the region over spiracles and anus. The postanal region is wanting in the abnormal male. *a.* anus; *a.d.* anal discal area; *c.f.* coxal fold; *a.♂*, male genital aperture; *m.d.* marginal discal area; *p.g.* preanal groove; *sp.* spiracle; *s.c.f.* supracoxal fold.

indicate the presence of underlying muscle insertions of the postanal region were not present. Instead of forming two sides of a triangle, the bases of the coxae were arranged in a circle so that the fourth coxae were very near together (Fig. 3B), and not wide apart as normally (Fig. 3A). The supracoxal fold followed the circular course of the coxae and joined its fellow of the other side (Fig. 3B, *s.c.f.*). There was no preanal groove. The spiracles followed the abnormal placing of the coxae and supracoxal groove (Fig. 3B, *sp.*). The fourth legs overlapped somewhat, and this fact together with the presence of the hump gave the tick such an awkward gait, that it failed to copulate when confined with a female for four days. Nevertheless, dissection proved that the genital system was well developed and the sperms normal. The hump was occupied mostly by the vasa deferentia and the rectal sac. The rectum was very wide and tubular for most of its length except for an occlusion adjacent to the bladder.

SUMMARY

During the examination of over 8000 specimens of *Ornithodorus moubata*, two cases of partial twinning (one male, one female) of the posterior region were noticed, and also a case of suppression of the postanal region in a male. All the freaks were viable, and the partial twins were normally fertile.

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THE LARVAL STAGES OF THE CELERY FLY (*ACIDIA HERACLEI* L.) AND OF THE BRACONID *ADELURA APII* (CURTIS), WITH NOTES UPON AN ASSOCIATED PARASITIC YEAST-LIKE FUNGUS

By D. KEILIN and P. TATE, *From the Molteno Institute, University of Cambridge*

(With 18 Figures in the Text)

Introduction

Curtis (1860) described the celery fly (*Acidia heraclei* L.) as a pest of cultivated celery in England, and since then it has become well known as a pest of this crop and very serious damage has been reported in some seasons (Edwards, 1914). It also occurs on parsnips, and although usually but little damage is done to this crop occasionally the damage is very severe (A. C. B., 1917). It is widely spread on the Continent of Europe and closely allied, or identical, species (*A. fratria* and *A. liogaster*) occur in North America (Doane, 1899), where the crop most damaged is parsnip.

The fullest account of the immature stages and of the biology of the fly is given by Gardner (1921). Gardner gives a list of recorded host plants, which, in addition to celery (*Apium graveolens*) and parsnip (*Pastinaca sativa*), includes a number of wild species of Umbelliferae and also several species of Compositae including the cotton thistle (*Onopordon acanthium*) and the creeping thistle (*Cnicus arvensis*), which, according to Edwards (1914), is frequently attacked and serves as a dangerous alternative host when growing near celery crops.

There is some dispute in the literature about the number of generations of the fly in the year, earlier authors (Ormerod, 1890; A. C. B., 1917) believing that there are two or more generations in a year, but Gardner (1921) states definitely that there are only two generations, one in April–June and the second from August onwards, although there may be considerable overlapping of the two generations. It has been stated that the first generation lives on wild umbelliferous plants and that only the second generation affects celery and parsnips (Anon. 1927).

Gardner gives the length of the various stages as follows: Adult flies in captivity live about 7 weeks; copulation occurs from 4 days after emergence, and the females lay up to 150 eggs about 2–11 days after copulation. Eggs hatch in 6–14 days in summer. The pupal period of the first generation is about 27 days; but the second generation of pupae hibernate in the soil at a depth of 3–4 in. and adults may not emerge until May of the following year. Sometimes pupation occurs in the leaves of the host plant.

The female fly lays eggs, two or three in quick succession, on the lower surface of leaves in cavities made beneath the cuticle with the ovipositor (Taylor, 1918). The larvae at first form narrow galleries in the parenchyma of the leaves, but as they grow they work in all directions and form irregular blisters on the leaves, and often neighbouring blisters coalesce to form large compound blisters (Taylor, 1918).

The puparium has been well described by Curtis (1860) and Gardner (1921). It is ovoid, about 5 mm. long by 2 mm. wide and the segments are deeply constricted. It is at first greenish but soon becomes pale yellowish or straw-coloured. It is very brittle owing to

the deposition of calcium carbonate, which derives from the calcospherites in the anterior pair of malpighian tubules at pupation (Keilin, 1921).

Gardner (1921) gives a list of the following hymenopterous parasites of *Acidia heraclei*: Braconids: *Alysia apii*, *Sigalphus flavipalpus*, *Opius cingulatus*, *Aspilota fuscicornis*, *Adelura apii*. Chalcids: *Pachylarthrus smaragdinus*, *Helicoptera flavicornis*. Ichneumon: *Hemiteles crassicornis*. Gardner (1921) also briefly described an unidentified larval parasite which he believed to be the larva of *Adelura apii*. Curtis (1860) refers to the parasites *Pachylarthrus smaragdinus* and *Alysia apii*, the latter of which is said to be an undoubted natural check on the excessive multiplication of the celery fly.

In the present paper a fuller description of the larval stages of *Acidia heraclei* than has hitherto been published will be given; and the first larval stage of *Adelura apii*, which has some features of special interest, will also be described. In addition, an account will be given of a yeast-like fungus, which has been found as a parasite in larvae of *Acidia heraclei*, and of its probable association with *Adelura apii*.

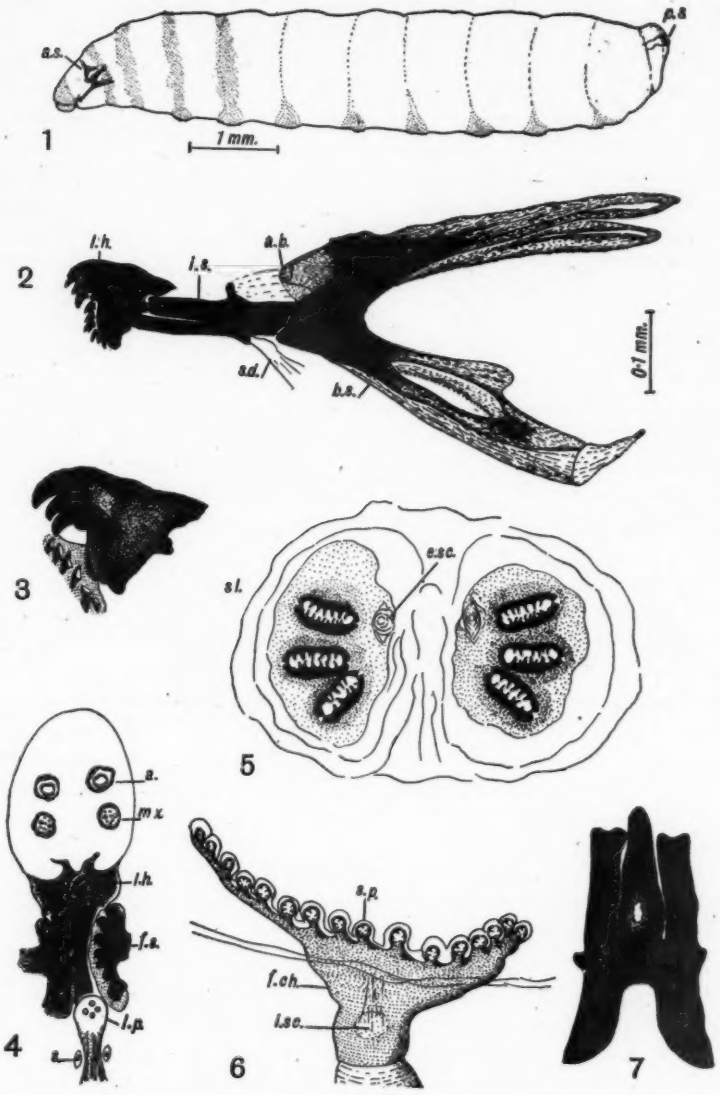
Larval stages of *Acidia heraclei*

Third stage larva. The mature third stage larva is about 1 cm. long and appears green owing to the contents of the gut showing through the body wall. The body wall of the larva is so transparent that the organs can be seen easily within the living larva. A striking feature is the presence of numerous, large, refractile calcospherites in the anterior pair of malpighian tubules (Keilin, 1921). The body, which tapers in front and is truncated posteriorly, is composed of a pseudocephalon, three thoracic and eight abdominal segments. The anterior borders of the three thoracic segments bear numerous spines arranged in oblique rows. Similar spinous areas encircle the anterior borders of the first two abdominal segments, but on abdominal segments 3–8 the spines are confined to lozenge-shaped areas on the ventral and ventro-lateral parts of the anterior borders of these segments. The remainder of the body wall is smooth and glistening (Fig. 1).

The anterior spiracles are situated dorso-laterally on the first thoracic segment (Fig. 1, *a.s.*). Each spiracle is composed of about 16–19 spiracular papillae, each of which has a minute spiracular slit at its apex (Fig. 6). The posterior spiracles are placed close together at the end of the eighth abdominal segment (Fig. 1, *p.s.*). Each spiracle has a slightly sclerotized peritreme in which there are three radiating, oval, spiracular clefts, the entrance to the felt chambers being guarded by a series of chitinous pegs projecting inwards from each side (Fig. 5). External scars are present but are inconspicuous (Fig. 5, *e.sc.*).

The transparency of the body wall allows the perispiracular glands to be seen and studied with ease in the living larva. The perispiracular glands of the anterior spiracles consist of a series of large glandular cells, corresponding in number to the number of spiracular papillae (Fig. 9, *gl.*). One glandular cell is connected with each papilla and a fine intracellular ductule (Fig. 9, *d.*) can be seen to carry the droplets of secretion from the interior of the cell to extrude it at the tip of the papilla beside the spiracular slit (Fig. 9, *g.o.*). The perispiracular glands of the posterior spiracles consist of groups of large glandular cells, three on each side, from which intracellular ductules carry the secretion to openings in the peritreme, one associated with each spiracular slit (Fig. 8).

Simple, one-segmented, antennae are borne on the anterior part of the pseudocephalon (Fig. 4, *a.*); and posterior to them there is a pair of maxillary palps, each formed of a



Figs. 1–7. *Acidia heraclei*. 1, mature third stage larva. 2, buccopharyngeal armature of third stage larva. 3, lateral hook, internal aspect. 4, ventral aspect of oral opening and associated sensory organs and fan-shaped, toothed, sclerites. 5, posterior spiracles. 6, anterior spiracle. 7, ventral aspect of intermediate sclerite of buccopharyngeal armature. Figs. 2–7 same scale.

sclerotized ring enclosing about six sensory papillae, two of which are larger than the other four (Fig. 4, *mx.*). Posterior to the oral opening there is a fleshy lobe bearing four sensory pits which represents the fused labial palps (Fig. 4, *l.p.*). There is a small sensory pit on each side of this lobe slightly farther back (Fig. 4, *s.*).

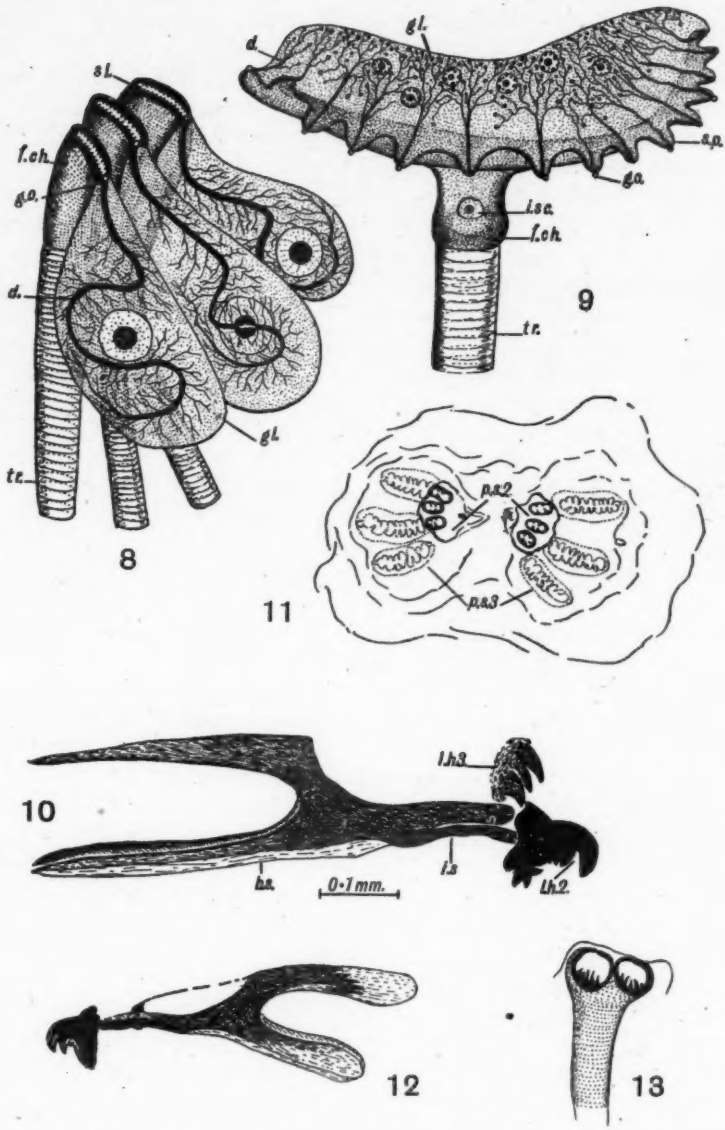
Buccopharyngeal armature. The buccopharyngeal armature is strongly developed and consists of a pair of lateral hooks, a strong intermediate sclerite and a basal sclerite (Fig. 2). The lateral hooks are roughly triangular with broad strong bases and have the anterior part produced into three strong, curved teeth (Fig. 2, *l.h.*; Fig. 3). Posteriorly they articulate with a very stout H-shaped median sclerite (Fig. 2, *i.s.*). A tongue-like process from the centre bar of this sclerite projects forwards and, anteriorly, lies between the bases of the lateral hooks (Figs. 2, 7). The opening of the common salivary duct pierces the base of this projecting piece, indicating that it is a development of the hypopharynx (Fig. 7). The intermediate sclerite articulates posteriorly with the basal sclerite. The basal sclerite is produced posteriorly into dorsal and ventral arms. The anterior part of the basal sclerite is well sclerotized, but the dorsal and ventral arms are weakly sclerotized (Fig. 2, *b.s.*). There is a well-developed dorsal bridge anteriorly (Fig. 2, *a.b.*). The ventral surface of the pharynx is smooth and is devoid of longitudinal pharyngeal ridges. Keilin (1915) has shown that this character is common to all truly parasitic cyclorrhaphous dipterous larvae and has termed such larvae 'biontophagous'. On each side of the lateral hooks there is an accessory fan-shaped sclerite bearing, ventrally, about ten strong curved teeth (Fig. 4, *f.s.*); and small cuticular teeth also border the oral opening.

Second stage larva. The second stage larva, besides being smaller, differs from the third stage larva in the following respects. The anterior spiracles contain fewer papillae, about 13–14. The posterior spiracles have each three small, oval, spiracular clefts, and their borders are produced into only two or three inwardly projecting pegs on each side (Fig. 11, *p.s.* 2). The buccopharyngeal armature is smaller, less strongly sclerotized, and the distinction between the intermediate and basal sclerites is not marked (Fig. 10). The lateral hooks differ in shape from those of the third stage larva, and, although each is produced into three teeth, the anterior tooth is much larger than the other two (Fig. 10, *l.h.* 2). The accessory fan-shaped sclerites have only three or four teeth in the second stage larva.

First stage larva. The first stage larva is metapneustic and the posterior spiracles are biforous (Fig. 13). The buccopharyngeal armature is small, weakly sclerotized, and the lateral hooks bear only two curved teeth (Fig. 12).

The early stages of *Adelura apii* (Curtis)

Larvae of *Acidia heraclei* are very frequently infected with the braconid *Adelura apii*. This is the commonest parasite of *Acidia heraclei* in the Cambridge region, where, in some seasons, more than 50% of celery-fly larvae harbour this parasite. The transparency of the *Acidia* larva allows the parasite to be seen readily within the living host. Three or more eggs of *Adelura apii* have been seen within one host larva, and the great enlargement of the eggs during development of the embryo, as is common during the development of eggs of parasitic Hymenoptera, could be followed in the living host. Although not uncommonly two or more young larvae of *A. apii* were seen in the same host larva, apparently only one of the parasites can attain full development, as large *Adelura* larvae



Figs. 8–13. *Acidia heraclei*. 8, perispiracular gland of a posterior spiracle as seen by transparency in the living larva. 9, perispiracular gland of anterior spiracle as seen by transparency in the living larva. 10, buccopharyngeal armature of second stage larva with the lateral hooks of the third stage developing (*l.h.*3). 11, posterior spiracles of second stage larva with the developing third stage spiracles showing beneath the cuticle (*p.s.*3). 12, buccopharyngeal armature of first stage larva. 13, posterior spiracle of first stage larva. Figs. 11–12 same scale.

were always found singly in the host larvae. The empty egg cases, eggs which had failed to develop, and dead *Adelura* or other hymenopterous larvae were often seen surrounded by phagocytic cysts and within these cysts the chitinized parts of the encysted body become very dark brown.

Specimens of *A. apii* have been bred out repeatedly from infected *Acidia* larvae, and there is no doubt that the first stage hymenopterous larva to be described is the larval stage of this species. It is the larval form which Gardner (1921) briefly described as that of an unknown larva, but probably of *Adelura apii*.

The first larval stage of *A. apii* has a number of very interesting characters and it will be described in detail. Although there are at least two other larval stages in the development of *A. apii* these later stages conform to the usual structure of the later stages of braconid larvae and need not be described in detail.

The first larval stage of *A. apii* is remarkable in that the larva has a strongly sclerotized head capsule, the body is very hairy and there is a long, curved, hairy, tail-like appendage. The larva closely resembles that of *A. gahani* described by de la Baume-Pluvinel (1915).

The first stage larva of *A. apii* has a dark brown head capsule nearly quadrangular in shape and a body composed of twelve, or, if the tail is considered to be a separate segment, of thirteen, segments. The head and tail are sharply curved and the body is semi-cylindrical in cross-section (Fig. 14). The orientation of the larva is obscure externally but it can be understood by comparison with *A. gahani* as described by de la Baume-Pluvinel (1915) and with *Diachasma crawfordi* as described by Keilin & Picado (1913). Keilin & Picado showed that, probably owing to more rapid growth of the ventral than the dorsal surface of *D. crawfordi*, the larva acquires a longitudinal curvature and is semi-cylindrical in cross-section, and that the concave surface, which appears to be ventral, is really dorsal and the true ventral surface is the convex one. De la Baume-Pluvinel (1915) found by studying the internal anatomy of *Adelura gahani* that the true orientation of this larva resembles that of *Diachasma crawfordi*, and that the tail and head are curved towards the dorsal surface.

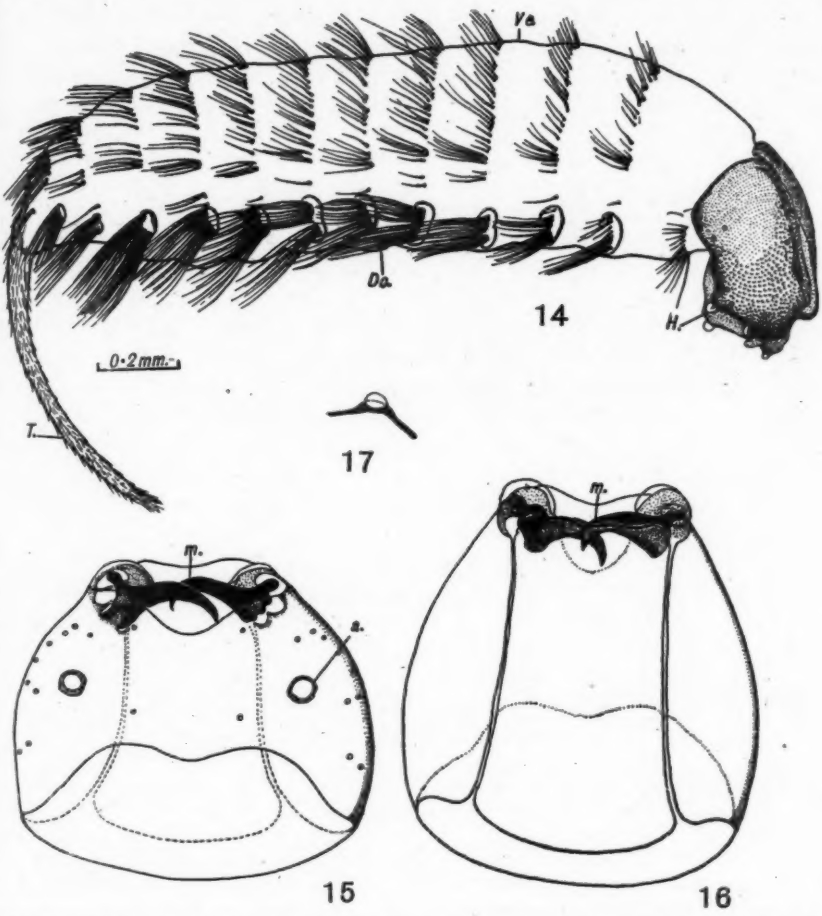
The true orientation of *Adelura apii* larvae corresponds to that described by the above authors for *A. gahani*, and *Diachasma crawfordi* and the tail and head are curved dorsally so that the true dorsal surface (Fig. 14, *Do.*) appears to be ventral, and the true ventral surface (Fig. 14, *Ve.*) appears to be dorsal. The lateral borders of the flattened dorsal surface are produced into a series of lobes, one on each side, on segments 2–11, and each lobe bears a dense tuft of long hairs (Fig. 14). The first and twelfth segments have rows of long hairs in place of the tufted lobes. Series of long hairs, interspersed with short sensory papillae, encircle the convex surfaces of segments 2–11 in line with the tufted lobes. There is a group of long hairs in the region of the anal opening on the twelfth segment. The tail is long and curved and is covered with long hairs which are agglomerated for most of their length but become free at the tips (Fig. 14, *T.*).

The head capsule is convex on its ventral surface (Fig. 16) and flattened, with the central region excavated, on the dorsal surface (Fig. 15). The ventral surface is covered by a median and two lateral sclerites which extend from the dorsal surface on which no sutures can be distinguished. The ventral surface of the head capsule is rugose for the anterior half (Fig. 14). Anteriorly, towards the dorsal surface there are two large, strong, curved, mandibular hooks which move in the horizontal plane (Figs. 15, 16, *m.*). The ventral surface is devoid of sensory processes, but on the dorsal surface there are rings

of thickened chitin, one on each side at the margin where the excavation begins. These rings support delicate domed membranes and represent antennae (Figs. 15, *a*, 17). There are eleven sensory pits on each side of the dorsal surface, two submedian and nine lateral.

The first stage larva has no functional tracheal system.

There are at least two further larval stages before pupation, as a later stage larva was found undergoing another moult. The later stages resemble those common to most



Figs. 14–17. *Adelura apii*. 14, first stage larva, lateral aspect—*Do.* dorsal surface; *Ve.* ventral surface. 15, dorsal aspect of head of first stage larva. 16, ventral aspect of head of first stage larva. 17, antenna of first stage larva. Figs. 15–17 same scale as Fig. 10.

parasitic hymenopterous larvae and are smooth, ovoid larvae with very much reduced mouthparts, but have a functional tracheal system with ten pairs of spiracles, two thoracic and eight abdominal. The first pair of thoracic spiracles is non-functional.

De la Baume-Pluvinel (1915) found that the larva of *Adelura gahani* undergoes at least two moults before pupation, but he apparently suspected that there was another moult

giving rise to a second stage hairy larva before the typical smooth hymenopterous form was attained. No evidence for this view has been found in the case of *A. apii*.

Yeast-like parasitic fungus

A parasitic, yeast-like fungus has been found to occur in the blood of some *Acidia heraclei* larvae. This fungus occurs as pullulating masses throughout the perivisceral space and is present in the form of isolated ovoid cells, budding cells, or short chains of cells. Its frequency varies amongst larvae from different areas and in different seasons, but, in general, the infection rate appears to be less than 10%. When present the infections become extremely heavy and the blood becomes filled with dense masses of the yeast

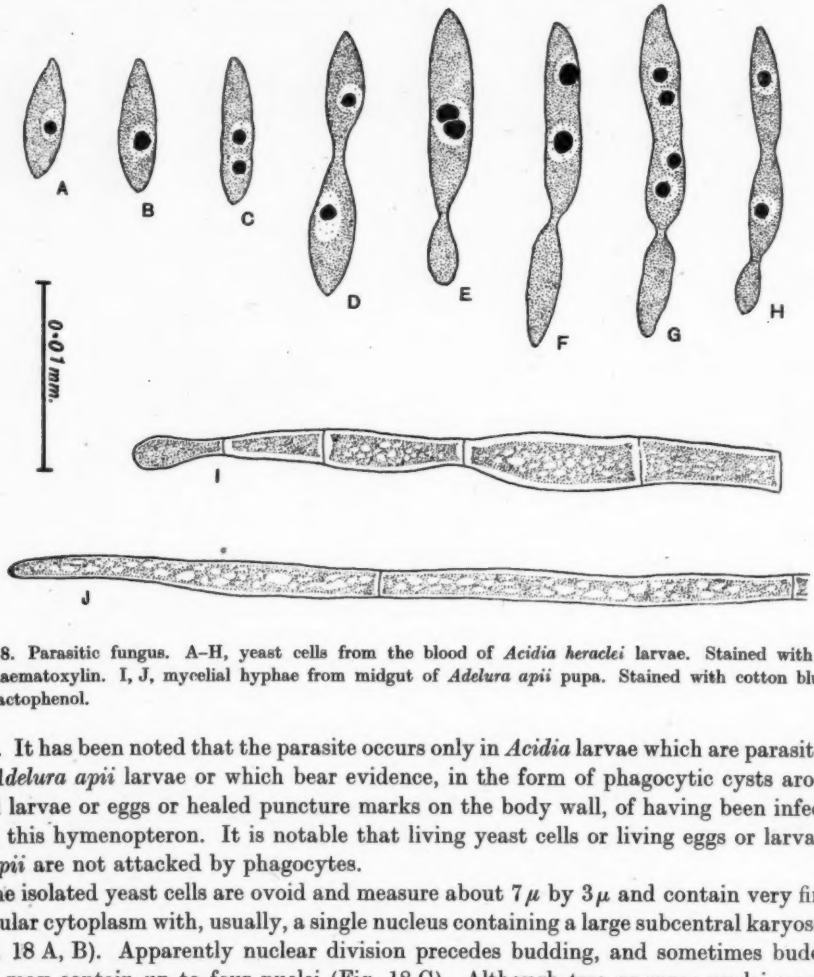


Fig. 18. Parasitic fungus. A–H, yeast cells from the blood of *Acidia heraclei* larvae. Stained with iron haematoxylin. I, J, mycelial hyphae from midgut of *Adelura apii* pupa. Stained with cotton blue in lactophenol.

cells. It has been noted that the parasite occurs only in *Acidia* larvae which are parasitized by *Adelura apii* larvae or which bear evidence, in the form of phagocytic cysts around dead larvae or eggs or healed puncture marks on the body wall, of having been infected with this hymenopteron. It is notable that living yeast cells or living eggs or larvae of *A. apii* are not attacked by phagocytes.

The isolated yeast cells are ovoid and measure about 7 μ by 3 μ and contain very finely granular cytoplasm with, usually, a single nucleus containing a large subcentral karyosome (Fig. 18 A, B). Apparently nuclear division precedes budding, and sometimes budding cells may contain up to four nuclei (Fig. 18 G). Although two or more nuclei may be present in the parent cell nuclear migration does not occur until the bud has attained

nearly its full size, and then the nucleus must pass into the daughter cell through the narrow neck connecting the parent cell with the bud (Fig. 18 D, E, F, G). Precocious budding before separation of daughter and parent cells may result in the formation of short chains of three or more cells (Fig. 18 H).

Acidia heraclei larvae parasitized by the yeast and by *Adelura apii* larvae may reach their full size and pupate normally. In some cases pupae of *A. apii* which had developed from *Acidia* larvae known to have been infected with the yeast were found upon dissection to have the midgut filled with a large mass of fungous mycelium consisting of fine septate hyphae (Fig. 18 I, J). As the *A. apii* larvae feed entirely on the host larvae it would appear that this mycelium must develop from the yeast cells which were present in the blood of the host larva, and that this mycelium is another stage in the development of the fungus parasitic in the *Acidia heraclei* larvae.

Attempts were made to cultivate the yeast stage of the fungus on a variety of media, but no growth was obtained. In the decomposing tissues of dead *Acidia* larvae, however, yeast cells were seen to send out septate hyphae, but growth soon stopped and the hyphae and yeast cells degenerated.

It has not been possible to follow the development of the fungus beyond the stage of mycelium in the gut of pupae of *Adelura apii*. The facts given above suggest that there is here an instance of a fungus which is parasitic for part of its life cycle in *Acidia heraclei* larvae and then undergoes further development in a hymenopterous parasite of the *Acidia* larvae. The close association of the yeast and *Adelura apii* infections and the fact that the yeast does not occur in the absence of infection with *A. apii*, suggests that the fungus may infect the adult female of *A. apii* by way of the mycelium in the gut of the pupa, and that, either in or together with the egg, the female *Adelura* infects the *Acidia heraclei* with the yeast when she oviposits in the host larva. So far we have not been able to prove this experimentally, but, if the supposition should prove to be correct, it would be a unique instance of a parasitic insect serving as a vector for a fungus parasitic in the host insect.

SUMMARY AND CONCLUSIONS

The larval stages of the celery fly, *Acidia heraclei*, have been described, and it is shown that this larva agrees with other biontophagous dipterous larvae in having the pharynx devoid of ventral ridges. The transparency of the larvae permits the internal anatomy to be seen clearly in the living larva, and by this means the structure of the perispiracular glands is clearly revealed.

The braconid *Adelura apii* occurs as a parasite of *Acidia heraclei* larvae, and its first stage larva is described in detail. This larva is densely hairy, has a long, curved, hairy, tail-like appendage and, by the more rapid growth of the ventral surface, it develops a dorsal curvature which obscures the true orientation so that the true dorsal surface appears externally to be ventral. In these respects the first stage larva of *Adelura apii* resembles that of *A. gahani* described by de la Baume-Pluvinel. The later larval stages of *A. apii*, of which there are at least two, are naked, lack the tail-like appendage and do not differ from the normal type of parasitic hymenopterous larvae.

A yeast-like fungus occurs as a parasite in the blood of *Acidia heraclei* larvae. It is always found associated with existing or abortive infection of the larvae with *Adelura apii*. Dense mycelial masses sometimes occur in the gut of *A. apii* pupae and are probably

derived from the yeast cells parasitic in the host larvae. It is suggested that this is a unique case of a fungus parasitic in a host larva (*Acidia heraclei*) undergoing part of its development in a parasitic braconid (*Adelura apii*), adult females of which transmit the fungus to the host larva during oviposition.

Key to lettering

a. antenna; *a.b.* anterior bridge; *a.s.* anterior spiracle; *b.s.* basal sclerite; *d.* ductule of glandular cell; *Do.* dorsal surface; *e.sc.* external scar; *f.ch.* felt chamber; *f.s.* fan-shaped sclerite; *gl.* glandular cell; *g.o.* opening of duct of perispiracular gland cell; *H.* head capsule; *i.s.* intermediate sclerite; *i.sc.* internal scar; *l.h.* lateral hooks; *l.h.*2, lateral hooks of second stage larva; *l.h.*3, lateral hooks of third stage larva; *l.p.* labial palps; *m.* mandibular hooks; *mx.* maxillary palps; *p.s.* posterior spiracles; *p.s.*2, posterior spiracles of second stage larva; *p.s.*3, posterior spiracles of third stage larva; *s.* sensory pit; *s.d.* salivary duct; *sl.* spiracular slit or cleft; *s.p.* spiracular papilla; *T.* tail-like appendage; *tr.* tracheal trunk; *Ve.* ventral surface.

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THE LARVA OF *PHAONIA PALPATA* STEIN (DIPTERA, ANTHOMYIDAE)

By P. TATE, *From the Molteno Institute, University of Cambridge*

(With 4 Figures in the Text)

Phaonia palpata Stein, 1897 (Séguy, 1923) appears to be a fairly common and widely distributed anthomyid. Séguy (1923) records it from a number of stations in France from June to October. Stein (1915) described it as *Aricia palpata*, and stated that it was not uncommon in Treptow in Germany, and that it had also been taken in other districts in Germany and in Sweden. Schnabl (1888) described a single male from Holland under the name *A. trigonalis*. Meade (1897), under the name *Hyetodesia trigonalis*, described it and said that it was not uncommon. There appears, however, to be no information in the literature regarding the immature stages of this fly.

A single puparium, from which a female *Phaonia palpata* emerged, was found in rotten wood of a willow tree at Grantchester, Cambridge, in April 1941. No further material has been found since, but it has been possible to determine the main anatomical features of the third stage larva from the exuvium recovered from the puparium after the fly had emerged.

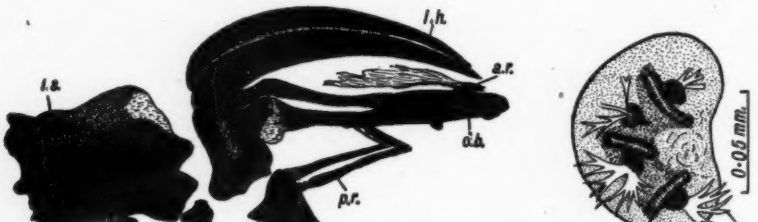
The buccopharyngeal armature of the third stage larva (Figs. 1, 2) is of the usual *Phaonia* type (Keilin, 1917). The basal sclerite (Fig. 2) is well sclerotized anteriorly and has deep lateral emarginations with weakly sclerotized latero-dorsal arms. The ventral surface of the pharynx is smooth and is devoid of longitudinal ridges; and there is a complete anterior dorsal bridge (*d.b.*). The intermediate sclerite (Fig. 1, *i.s.*) is short, very deep and is very strongly sclerotized. The lateral hooks (*l.h.*) are long, curved, sharply pointed and lie close together. Stout oral bars (*o.b.*) extend forward from the bases of the lateral hooks to unite anteriorly; about one-quarter of their length from the anterior end they have, each, a stout blunt knob on the ventral edge. There is a stout median ventral arc (*m.v.a.*) joining the bases of the lateral hooks, and from its anterior margin a posterior ribbon (*p.r.*) extends forwards on each side and then bends sharply back upon itself to join the mid-ventral part of the oral bar. Above the anterior half of the oral bars there is a weakly sclerotized anterior ribbon (*a.r.*).

The posterior spiracles are small, have weakly sclerotized peritremes, and each has three small, narrow, slightly curved spiracular slits arranged radially (Fig. 3). The slits (*sl.*) are guarded by numerous fine inwardly projecting teeth on each side. Four groups of flattened, branched, radiating hairs arise in relation to the openings of the peri-spiracular glands (*g.h.*).

The perianal plate (Fig. 4) is broad, backwardly curved and has an anterior median inflexion and two lateral inflexions on the posterior margin.

No further details could be made out from the material available, but it is evident from the structure of the buccopharyngeal armature that the larva is carnivorous in habit. This is shown by the absence of ventral pharyngeal ridges; and the presence of sharply pointed, opposed lateral hooks with their associated oral bars and anterior and posterior ribbons. Keilin (1917) has shown that these characters indicate a carnivorous mode of life in larvae possessing them.

Keilin (1917) showed that of the eleven species of the genus *Phaonia* of which there was information about the biology of the larval stages, the larvae of four species are certainly carnivorous. These species are *P. cincta*, *P. goberti*, *P. variegata* and *P. trimaculata*. More recently, another species, *P. mirabilis*, has been shown to be carnivorous in the larval stage (Tate, 1935); and Keilin believed that, judging by the structure of the buccopharyngeal armature, larvae of *P. parenti* (=*P. canescens* Stein, 1916) and of *P. nepenthincola* are also carnivorous. Larvae of the species *P. signata*, described as accidental parasites of *Carabus*, are probably really carnivorous according to Keilin; but



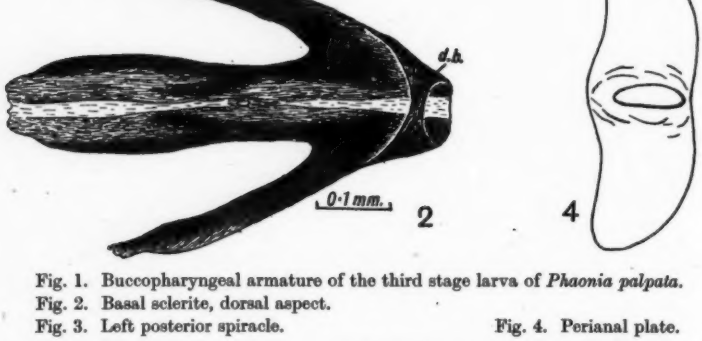


Fig. 1. Buccopharyngeal armature of the third stage larva of *Phaonia palpata*.
Fig. 2. Basal sclerite, dorsal aspect.
Fig. 3. Left posterior spiracle.
Fig. 4. Perianal plate.

a.r. anterior ribbon; *d.b.* dorsal bridge; *g.h.* hairs associated with opening of perispiracular glands; *i.s.* intermediate sclerite; *l.h.* lateral hooks; *m.v.a.* median ventral arc; *o.b.* oral bar; *p.r.* posterior ribbon; *sl.* spiracular slit.

there is insufficient data about *Phaonia turpis*, *P. laeta* and *P. querceti* to decide the mode of life of the larvae. Keilin finally suggested that the larvae of all species of *Phaonia* would prove to be carnivorous in habit. It is interesting that the absence of larval trimorphism, a third stage larva hatching from the egg, has been shown in two species of *Phaonia*, in *P. mirabilis* by Tate (1935) and in *P. variegata* by Thomson (1937); and this may prove to be true of all species of the genus when more is known about their early development.

The structure of the buccopharyngeal armature of *P. palpata* is very similar to that of *P. variegata* as described by Keilin (1917) and by Thomson (1937), but differs in the fact that the anterior ribbons are devoid of sharp teeth such as occur in *P. variegata*

and also in *P. cincta*, *P. goberti* and *P. mirabilis*. The blunt, ventrally projecting knob on the oral bars of *P. palpata*, together with the absence of sharp teeth on the anterior ribbons, serves to distinguish larvae of this species from the larvae of all other species which have so far been described.

The structure of the posterior spiracles of *P. palpata*, which are small, not heavily sclerotized and have three narrow, slightly curved radiating slits, is very similar to that of *P. variegata*.

SUMMARY

The larva of *Phaonia palpata* closely resembles that of *P. variegata* in the structure of the buccopharyngeal armature and of the posterior spiracles. The absence of sharp teeth on the anterior ribbons and the presence of a blunt knob on the ventral edge of the oral bars distinguish the larva of *P. palpata* from larvae of other species of *Phaonia*.

I wish to express my thanks to Mr J. E. Collin, Newmarket, for identifying the imago of *P. palpata*.

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THE ANATOMY OF THREE DIGENETIC TREMATODES, *SKRJABINIELLA ACULEATUS* (ODHNER), *LECITHOCHIRIUM RUFOVIRIDE* (RUD.) AND *STERRHURUS FUSIFORMIS* (LÜHE) FROM *CONGER CONGER* (LINN.)*

By DILYS O. JONES, M.Sc., *Department of Zoology, University College of Wales, Aberystwyth*

(With 11 Figures in the Text)

The material used in this investigation was obtained from the stomach and intestine of a *Conger conger* (Linn.) caught at Millport, Buteshire,† and at Milford Haven, Pembrokeshire. *Skrjabiniella aculeatus* (Odhner), a gasterostomid worm, was found in the anterior part of the intestine, and *Lecithochirium rufoviride* (Rud.) and *Sterrhurus fusiformis* (Lühe), both hemiurids, were in the stomach.

The worms were fixed immediately on removal from the host in Gilson's fluid. A few which were fixed in Mann's osmo-sublimate did not give better results. For the investigation whole mounts and serial sections were used, both of which were stained with Ehrlich's haematoxylin and the latter counterstained with eosin. Unstained whole mounts were best for details of dermal spines in *Skrjabiniella aculeatus*. The sections were cut from 6 to 8μ in transverse and in tangential and facial longitudinal planes. In addition, it was possible to make observations on the living specimens of *Lecithochirium rufoviride* and *Sterrhurus fusiformis* under a coverslip with the aid of a binocular microscope. All measurements were made by means of an ocular micrometer from fixed material.

Skrjabiniella aculeatus (Odhner 1905) (Figs. 1, 2, 9)

Synonymy. 1870. *Gasterostomum crucibulum* (Rud.).
1876. *Gasterostomum armatum* Molin.
1905. *Prosorhynchus aculeatus* Odhner.
1928. *Skrjabiniella aculeatus* (Odhner).

Skrjabiniella aculeatus was first described by van Beneden (1870) and later by Odhner (1905) and Nicoll (1910). None of the descriptions gave full details of histology especially of the genital ducts, and only van Beneden included a figure. The writer therefore proposes to give below an amplified account, with illustrations, based upon a study of whole mounts and serial sections.

External features (Fig. 1). The worm is almost elliptical, being slightly more pointed posteriorly and measures $1{\cdot}3 \times 0{\cdot}66$ mm. The body is only slightly flattened dorso-ventrally. At the anterior end is an oval rhynchus which when retracted is twice as broad as long, measuring $0{\cdot}11 \times 0{\cdot}205$ mm., giving the body a truncated appearance. The entire surface

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† For these specimens the writer is indebted to Mr Elmhirst, Director of the Marine Biological Station, Millport.

is covered by a thin cuticle which is armed by diagonal rows of large scale-like spines. The posterior ends of the latter are pointed and project through the cuticle at an acute angle. The spines on the rhynchus and anterior end measure 0·014 × 0·009 mm., while over the remainder of the body they are 0·011 × 0·008 mm.

The mouth is situated ventrally in the middle line about a quarter of the total body length from the posterior end. It is surrounded by a muscular region which has been incorrectly described as an oral sucker but which really lies in the wall of the digestive

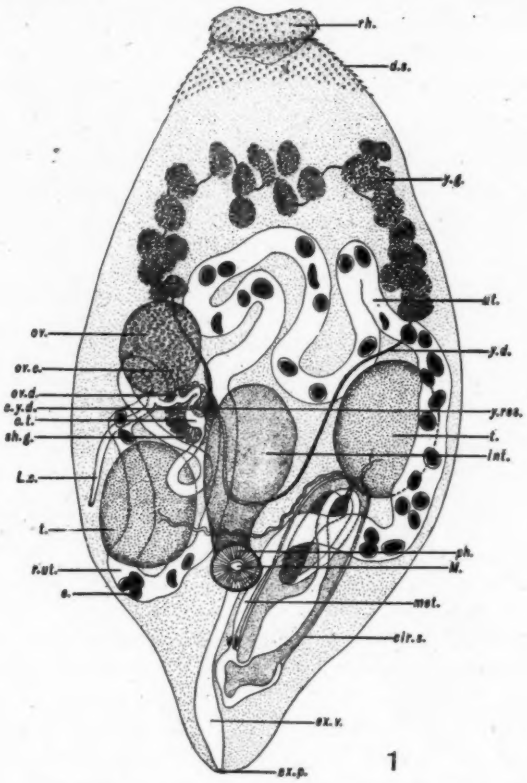


Fig. 1. *Skrjabiniella aculeatus.* General anatomy from ventral surface, dermal spines shown only at anterior end.

tube and is a large pharynx (Fig. 9). The genital aperture is situated ventrally behind the mouth, 0·176 mm. from the posterior end. The excretory aperture is at the extreme posterior tip of the body.

Muscular system. The musculature is typical, with circular, then longitudinal and then oblique muscles forming the body wall. The longitudinal and oblique fibres are arranged in bundles; the former cut each other at right angles and the latter meet at a more acute angle anteriorly than posteriorly, but the angle is always more than a right angle. None of these muscles in the body wall is deflected in the region of the pharynx which is further proof that there is no oral sucker. Dorso-ventral muscles are also present espe-

cially in the region of the intestine and genitalia. The muscles of the rhynchus are simple and resemble closely those of *Prosorhynchus uniporus* Ozaki (Table 1). In *Skrjabiniella aculeatus* there is a thin muscular wall enclosing stout longitudinal muscles between which are loose parenchyma cells and unicellular gland cells. The longitudinal muscles appear to be arranged in ten bundles in sagittal section. These serve to expand the rhynchus so that it may reach the lining of the host's intestine; by the subsequent contraction of the central fibres a vacuum is created, the rhynchus thus serving as an organ

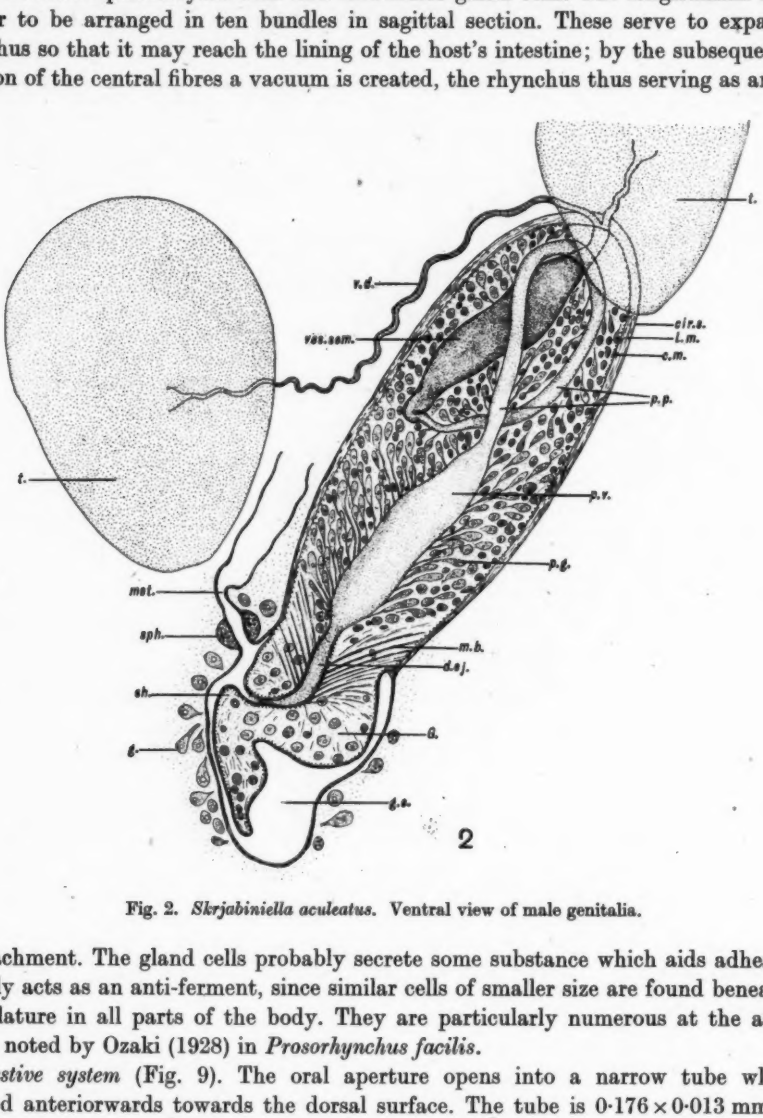


Fig. 2. *Skrjabiniella aculeatus.* Ventral view of male genitalia.

of attachment. The gland cells probably secrete some substance which aids adhesion or possibly acts as an anti-ferment, since similar cells of smaller size are found beneath the musculature in all parts of the body. They are particularly numerous at the anterior end as noted by Ozaki (1928) in *Prosorhynchus facilis.*

Digestive system (Fig. 9). The oral aperture opens into a narrow tube which is directed anteriorwards towards the dorsal surface. The tube is 0·176 × 0·013 mm., and lined throughout by a cuticle continuous with that covering the external surface. It is divided into two portions equal in length; that nearest the oral aperture is the pharynx which has highly muscular walls forming a bulb 0·095 mm. in diameter, while the second half is the oesophagus with less muscular walls. Opening into the oesophagus are numerous

unicellular gland cells arranged in two lateral groups in the parenchyma. These probably secrete a digestive ferment. The oesophagus opens into a sacciform intestine 0·176 × 0·110 mm. with its blind end directed anteriorly. This has thinner walls than any other part of the digestive canal and is not lined by cuticle; it is therefore the absorptive region. The muscles in its wall are continuous with those of the oesophagus, pharynx and body wall so that the longitudinal fibres are outside the circular ones. The innermost lining of the intestine consists of small, closely packed epithelial cells which are columnar in shape with basal nuclei and distal vacuoles. They probably function for intra- as well as extracellular digestion, since many of them contain foreign particles.

Excretory system (Fig. 1). The posterior excretory pore leads into a wide vesicle situated dorsally and slightly to the left of the middle line. In the specimens examined it was traced only as far as the pharynx. It is fairly uniform in width with an internal lining membrane on the surface of which minute globules, probably, in part excretory products, could be seen in facial section.

Genital system (Figs. 1, 2). (1) *Male.* There are two testes, one on either side in the posterior half of the body, the left slightly in advance of the right. They extend through the entire thickness of the body and are longitudinally elongate measuring 0·220 × 0·231 mm. The right testis is close to the intestine with its posterior border on a level with the mouth while it is overlapped antero-dorsally by the female genitalia (Fig. 1). The left testis extends anteriorly to the middle of the body and is overlapped postero-dorsally by the anterior margin of the cirrus sac which is situated entirely on the left side of the body in this species.

The male sex cells escape by a narrow convoluted vas deferens which leads from the mid-dorsal region of each testis. Owing to the peculiar disposition of the cirrus sac the left vas deferens has a very short course while the right travels transversely dorsal to the oesophagus and then turns anteriorwards along the right border of the cirrus sac. Both vasa deferentia open into the latter at its anterior extremity where they join to form a vesicula seminalis 0·035 mm. broad with delicate muscular walls (Fig. 2). There is no part of the vesicula seminalis outside the sac as stated by Nicoll (1910), although such a condition is described by Lebour (1908) for *Prosorhynchus squamatus* Odhner (Table 1). The subsequent course of the male system is all contained within the cirrus sac which has a thick muscular wall consisting of stout longitudinal fibres on the outside and more delicate circular muscles internally. It measures 0·352 × 0·121 mm. The vesicula seminalis occupies a central position in the anterior half of the cirrus sac and communicates posteriorly through a narrow sphincter with the narrow pars prostatica with delicate muscular walls lined by relatively large, thin-walled, compact cells. The pars prostatica describes a complete loop in the anterior end of the cirrus sac, ventral to the vesicula seminalis, and then takes up a central position in the sac posterior to the latter. Here it widens to a diameter of 0·033 mm., forming the prostatic vesicle which is also lined by thin-walled cells. Opening into the pars prostatica and the prostatic vesicle are numerous unicellular prostatic gland cells, 0·017 mm. in diameter, which fill the remaining cavity of the cirrus sac. The prostatic vesicle opens abruptly into a short narrow muscular tube, the ductus ejaculatorius which measures 0·033 × 0·011 mm. and is bounded by outer circular and inner longitudinal muscles, the reverse of the arrangement in the wall of the cirrus sac. Inserted obliquely into its wall and terminating more anteriorly in the distal wall of the cirrus sac are four sets of powerful extrinsic muscles. The ejaculatory

duct opens into the genital sinus immediately ventral to the female opening. This male aperture is at the base of a long, curved 'genital tongue' 0·035 × 0·007 mm., which occupies a dorsal position in the sinus with its distal tip pointing ventrally towards the common genital aperture. Proximally it bears a 'shoulder' which lies between the male and female openings. At the distal end of the ejaculatory duct, ventral and anterior to the shoulder, a rounded mass of sperms could often be seen in sections. The sperms appear cemented together probably by a secretion from the gland cells which surround the genital atrium and are abundant in the 'genital tongue'. Judging by its position it is probable that the latter functions also to prevent self-fertilization; it clearly cannot function as a penis since it is not penetrated by the ejaculatory duct. The genital sinus has a diameter of 0·110 mm. and opens by a small pore to the exterior.

(2) *Female* (Fig. 1). The ovary is situated on the right side of the body in front of and above the right testis. It is subglobular in shape measuring 0·154 × 0·143 mm. with its long axis running longitudinally. Histologically, it resembles that of other Digenea, the largest ova being 0·009 mm. in diameter. The most mature ova were found in the ovicap which is in the dorsal region of the ovary near its posterior border. It passes into a narrow oviduct 0·004 mm. broad which proceeds posteriorwards in a dorsal position. Immediately behind the ovary it receives Laürer's canal which is still more dorsal and has a diameter of 0·121 mm. It is lined throughout by pyramidal cells which present a trabeculate appearance in oblique section. It contains numerous spermatozoa near its junction with the oviduct, whence it curves round and passes to the outside through a small muscular aperture on a level with the centre of the right testis in a dorso-lateral position. Its function therefore appears to be the expulsion of surplus spermatozoa.

After receiving Laürer's canal, the oviduct bends round to the left of the ovary and here receives dorsally the common yolk duct from the vitelline glands and then widens immediately to form the ootype which is relatively large and in proportion to the large size of the ripe eggs. It is lined by a delicate cellular membrane and receives a secretion from the shell glands.

The vitelline glands consist of a number of yolk follicles 0·05 mm. in diameter arranged in the form of an arc in the anterior third of the body. In this species the arc is divided into three groups, one anterior and two antero-lateral, the anterior one being the most ventrally placed. Each group contains 8–10 follicles, each of which is made up of cells which are largest towards the centre. The yolk granules inside the cell do not take up the stain and appear yellow; they escape into the ducts by the rupture of the cell. Each follicle has one small duct, and these open alternately on either side of each of the two main yolk ducts. These latter are 0·008 mm. in diameter and occupy a dorsal position throughout most of their course. The follicles to the left of the middle line drain into the left yolk duct and those to the right into the right yolk duct. The left yolk duct passes backwards right of the left testis and then transversely above the oesophagus to loop forwards again to a position dorsal to the shell gland. Here it is joined by the right yolk duct which has a much shorter course mainly dorsal to the ovary. Where the two main yolk ducts join a yolk reservoir is formed from which a short common yolk duct passes ventrally into the end of the oviduct near the ootype.

The shell gland surrounding the ootype is compact and globular with a diameter of 0·08 mm. It is composed of numerous unicellular gland cells with large nuclei and abundant cell contents opening independently into the ootype. The shell gland lies left

of the ovary and partly overlaps it postero-dorsally; it is separated from the surrounding parenchyma by a thin muscular limiting layer which probably functions to press the eggs onwards from the ootype.

From the ootype the female duct proceeds as the uterus which forms a number of coils posterior and ventral to the ovary. This part functions as a receptaculum uterinum and contains numerous spermatozoa as well as eggs. The uterus then turns directly anteriorwards as a straight tube dorsal to the digestive canal and then forms a number of loops between the intestine and the arc formed by the vitellaria. It then proceeds posteriorly ventral to the left testis as far as the cirrus sac. Here it crosses beneath the cirrus sac and runs parallel to its right border to open into the genital sinus dorsal and to the right of the aperture of the ejaculatory duct. For a distance almost equivalent to the length of the cirrus sac the walls of the uterus are especially thick and muscular with a cuticular lining and smaller cavity. This region is an ill-defined metraterm and bears at its aperture a globular sphincter which regulates the passage of eggs to the outside. The exact number of coils of the uterus varies with age, but the general course is constant for the species. The ripe eggs are relatively large and measure $0{\cdot}027 \times 0{\cdot}018$ mm. They are yellowish with one end slightly pointed and many showed signs of segmentation within the uterus.

Comments on nomenclature

Skrjabiniella aculeatus (Odhner) is a typical member of the suborder Gasterostomata. This suborder was first created by Odhner (1905) to include those digenetic trematodes with a mouth situated on the ventral surface of the body as opposed to the anterior position characteristic of the Prostomata. Amongst them are forms whose exact positions with regard to classification have long been confused. Odhner included only one family in his suborder, the family Gasterostomidae, in which he recognized two genera. Those with a sucker at the anterior end he grouped together in the genus *Gasterostomum*, while for those with a retractile rhynchus or proboscis instead of a sucker he created the new genus *Prosorhynchus*.

Nicoll (1914) divided Odhner's genus *Gasterostomum* into three new genera, *Bucephalus* Baer, *Bucephalopsis* Diesing and *Rhipidocoyle* Diesing. He stressed the fact that he had found in *Rhipidocotyle* a fan-shaped hood, which he thought might represent a vestigial or rudimentary rhynchus, as well as a small sucker. Since the creation of the genus *Prosorhynchus* rests upon the assumption that the rhynchus and the sucker are homologous and therefore not found together in any one form, a further investigation of *Rhipidocotyle* and allied types should prove useful. But so far as present information suggests there seems to be good reason to place forms possessing a rhynchus in a separate genus. In spite of *Rhipidocotyle*, Nicoll (1914) raised Odhner's two genera to subfamily rank and they become, as tentatively suggested by Odhner himself, the subfamilies Bucephalinae (=Gasterostominae) in place of *Gasterostomum* and Prosorhynchinae in place of *Prosorhynchus*.

Issaitschikow (1928) revised the suborder Gasterostomata. He accepted the subfamilies Gasterostominae and Prosorhynchinae, but pointed out another feature of subfamily importance in addition to the rhynchus or sucker, viz. the arrangement of the yolk follicles. Thus he defined the subfamily Gasterostominae as having an anterior sucker and yolk follicles in two lateral groups, and the subfamily Prosorhynchinae with anterior rhynchus and yolk follicles forming an arc anteriorly. He also redefined the genus

Prosorhynchus as Prosorhynchinae with the testes arranged in tandem and with a mouth anterior to them. For those members of the suborder with the testes arranged symmetrically on either side of the body and a more posterior mouth he created the new genus *Skrjabiniella* with *S. aculeatus* (=*Prosorhynchus aculeatus*) as type-species.

This definition of the genus *Skrjabiniella* was accepted by Pigulewsky (1931). He revised the Prosorhynchinae again and recognized that the types included here could again be divided into two groups on the form of the yolk glands in the same way as Issaitschikow divided the subfamilies. He therefore created two tribes within the Prosorhynchinae: Prosorhynchia with oval bodies and yolk follicles in the form of an anterior arc, and Gotonia with elongated bodies and yolk follicles in two lateral groups. He therefore cancelled out the view of Issaitschikow that the arrangement of yolk follicles is a feature of subfamily rank, and so leaves Nicoll's definition of the two subfamilies as the most feasible method of classification.

Subsequent writers have not accepted this new generic name *Skrjabiniella* for *Prosorhynchus aculeatus*. Manter (1934) considered *Skrjabiniella* to be a synonym of *Prosorhynchus*, while Yamaguti (1937) regarded it as a subgenus of *Prosorhynchus*.

Table 1. *List of species of the genus* Prosorhynchus *Odhner showing subdivision into two genera*—Prosorhynchus *s.str. and* Skrjabiniella

Species	Arrangement of yolk follicles	Arrangement of testes	Shape of body	Shape of rhynchus	Position of mouth in relation to anterior testis
Prosorhynchus Ozaki Manter	Two lateral groups	In tandem	Elongated	Oval	Posterior
Prosorhynchus crucibulum (Rud.)	Anterior arc	Symmetrical	,,	Conical	Anterior
Genus *Skrjabiniella*:					
Prosorhynchus aculeatus Odhner	Anterior arc	Symmetrical	Elliptical	Oval	Posterior
Prosorhynchus squamatus Odhner	,,	,,	,,	,,	,,
Prosorhynchus uniporus Ozaki	,,	,,	,,	,,	,,
Prosorhynchus grandis Lebour	,,	,,	,,	,,	,,
Genus *Prosorhynchus* s.str.:					
Prosorhynchus facilis (Ozaki)	Two lateral groups	In tandem	Elongated	Conical	Anterior
Prosorhynchus cortai Trav. Art. & Per.	,,	,,	,,	,,	,,
Prosorhynchus platycephali (Yamaguti)	,,	,,	,,	,,	,,
Prosorhynchus Manteri Sriv.	,,	,,	,,	,,	,,
Prosorhynchus arabiana Sriv.	,,	,,	,,	,,	,,

In the present work a list has been compiled of eleven species of *Prosorhynchus* (Table 1) with their most significant points of contrast. From this table the original genus *Prosorhynchus* as defined by Odhner can be divided into two definite groups upon five characters of generic importance, viz. the arrangement of yolk follicles, position of testes relative to each other, shape of body, shape of rhynchus, and position of mouth relative to testes. Each of these characters is equally constant, and upon them all the same four species are separated from the remainder of the genus, viz. *Prosorhynchus aculeatus*, *P. squamatus*, *P. uniporus*, and *P. grandis*, although Issaitschikow did not separate out any types other than *P. aculeatus*. *P. Ozaki*, and *P. crucibulum* are the only ones which at present appear not to fit into this scheme, but since they are both inadequately described further work upon them would be essential to complete this division. Pigulewsky (1931) includes the arrangement of yolk follicles as a diagnostic feature of the tribe, while he accepts the arrangement of the testes and position of the mouth as features distinguishing the genus

Skrjabiniella. All three characters as well as shape of body and shape of rhynchus have been shown in the present survey to be of equal importance, since the genus divides itself into the same two groups on each feature. The present writer considers that at the moment we cannot assume more than the rank of genus for these characters, and the following key to the genera of the subfamily Prosorhynchinae is suggested:

Yolk follicles arranged in anterior arc, testes symmetrically arranged on either side of the body, body elliptical, rhynchus oval, mouth behind anterior testis. Genus SKRJABINIELLA

Yolk follicles arranged in two lateral groups, testes arranged in tandem, body elongated, rhynchus elongated, mouth in front of anterior testis. Genus PROSORHYNCHUS

According to the present analysis *Skrjabiniella* is a separate genus not synonymous with nor a subgenus of *Prosorhynchus*.

Lecithochirium rufoviride (Rud. 1819) (Figs. 3–6)

Synonymy. 1819. *Distomum rufoviride* Rud.
1899. *Hemiurus rufoviride* (Rud.).
1901. *Lecithochirium rufoviride* (Rud.).
1907. *Distomum ocreatum* Molin.
1907. *Lecithochirium* s.str. *rufoviride* (Rud.).

Lecithochirium rufoviride (Rud.) has been described several times, the most detailed accounts being those of Lühe (1901) and Looss (1907). The descriptions still need amplification especially in relation to the genitalia, since the homologies of the ducts, which are important in Looss's classification, are disputed by subsequent writers. Looss regards *Lecithochirium rufoviride* as the type-species of his genus *Lecithochirium* s.str.

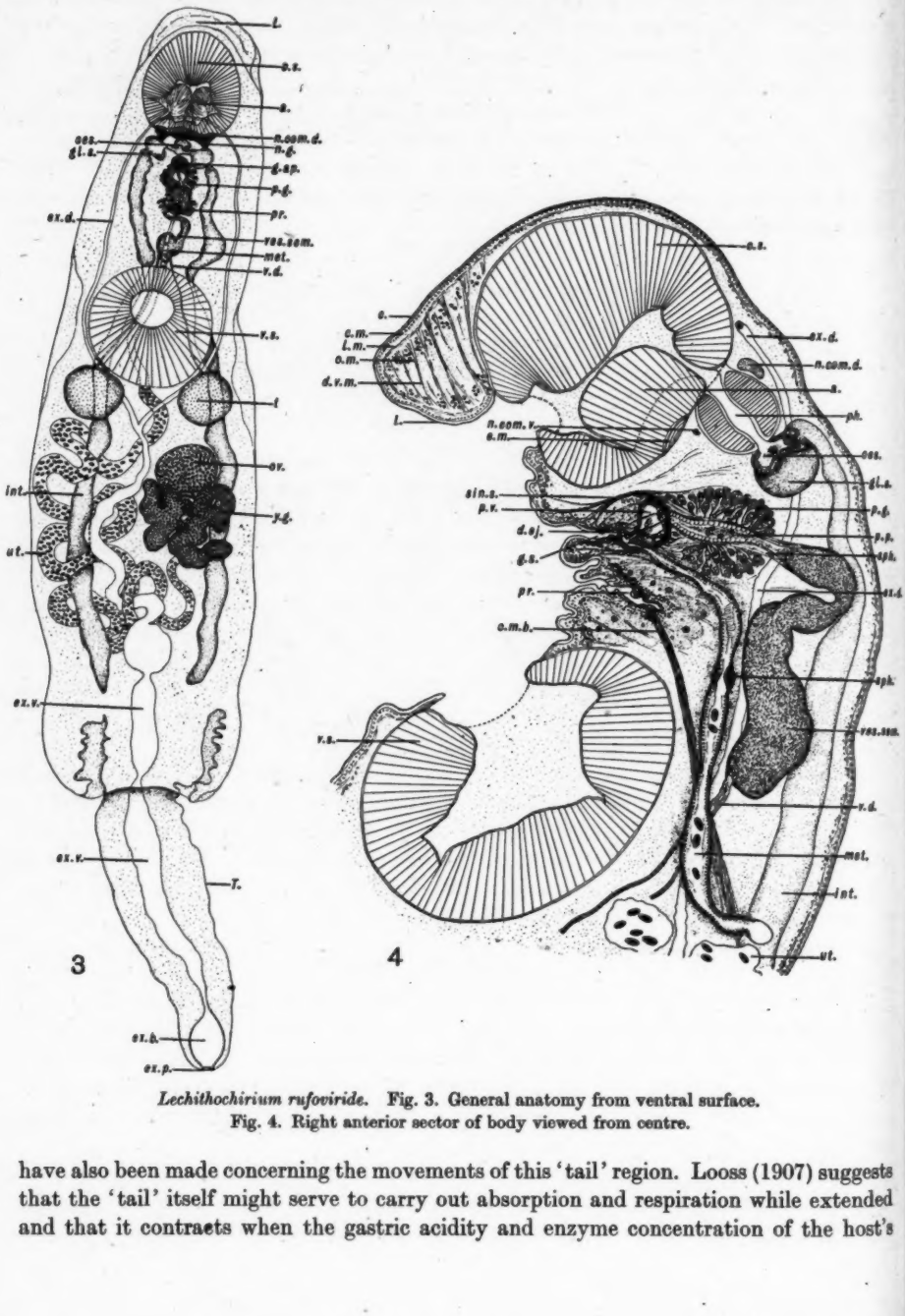
External features (Fig. 3). In the living condition the body is of a deep brownish orange colour. It is cylindrical in shape with a narrow 'tail' region of one-third the total body length. When the 'tail' is extended the worm is 4–6 mm. long and the maximum width is 1·7 mm. The ventral surface of the 'tail' is continuous with the ventral surface of the body. The body surface is smooth, without spines, and the cuticle is thickest ventrally between the two suckers.

The oral sucker is subterminal and lies completely ventrally, since it is bounded anteriorly by a muscular lip. The sucker is almost circular with a diameter of 0·7 mm., while the lip is 0·2 mm. long and flexed towards the ventral surface. The aperture of the oral sucker is hexagonal in outline measuring 0·5 mm. across and 0·3 mm. long. Inside this aperture and attached to the posterior rim of the sucker is a pair of muscular arches 0·25 mm. in diameter and one on either side of the pharynx.

Posterior to the oral sucker and separated from it by about one-third of the body length is the ventral sucker or acetabulum which is 0·79 × 0·83 mm. Its external aperture is circular with a diameter of 0·25 mm. The size ratio of oral to ventral suckers is 1 : 1·14. In front of the acetabulum is a pronounced muscular pit, the 'cervical groove' of Looss, or preacetabular pit which resembles an accessory sucker except that its fibres are not definitely demarcated from the surrounding musculature and parenchyma. The common genital aperture lies midway between this pit and the oral sucker. At the tip of the 'tail' is the aperture of the excretory system.

In the living condition the preacetabular portion of the body expands a great deal and when at rest becomes arched antero-posteriorly, the concavity being ventral with the oral sucker opposed to the ventral acetabulum. When placed in saline, the writer

detected rhythmic contractions and extensions of the 'tail' which suggests that this movement facilitates the passage of excretory products to the exterior. Other suggestions



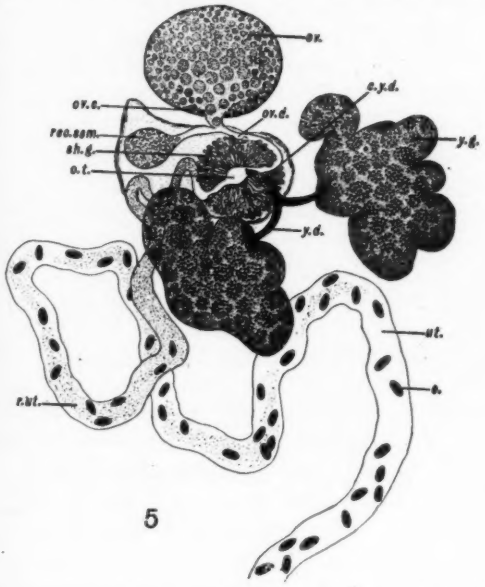
Lechithochirium rufoviride. Fig. 3. General anatomy from ventral surface.
Fig. 4. Right anterior sector of body viewed from centre.

have also been made concerning the movements of this 'tail' region. Looss (1907) suggests that the 'tail' itself might serve to carry out absorption and respiration while extended and that it contracts when the gastric acidity and enzyme concentration of the host's

digestive tract is high. Lloyd (1938) suggests that the preacetabular pit may detect chemical changes in the environment thus controlling the movements of the 'tail'.

Muscular system (Figs. 4, 6). The muscular system is well developed as in other Hemiuridae. The muscles of the body wall are typical with circular outside, then longitudinal and then oblique fibres, and in the region of the anterior lip, preacetabular pit and distal genital ducts, dorso-ventral muscles. The anterior lip, preacetabular pit and the 'tail' are particularly muscular. Special muscles are developed in relation to the two suckers which are themselves muscular and definitely delimited from the body wall and parenchyma.

The anterior lip (Fig. 4) is bounded by pronounced circular, longitudinal and oblique muscles. Between the two layers of oblique muscles stretch well-defined dorso-ventral



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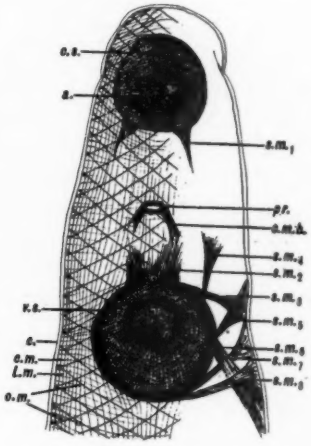

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Lecithochirium rufoviride. Fig. 5. Ventral view of female genitalia. Vitellaria displaced for clarity. Fig. 6. Ventral view of anterior end showing musculature of body wall and suckers. Ventral sucker muscles drawn on left side only, body wall muscles on right.

fibres, while in the parenchyma between them are scattered glandular cells. The lip is therefore thick and fleshy and overhangs the oral sucker ventrally.

In the region of the preacetabular pit the oblique and the dorso-ventral muscles are the best developed. One pair of oblique muscles is particularly strong (Fig. 4). They are inserted on the antero-lateral border of the pit and directed backwards dorsally over the ventral sucker and inserted in the dorsal body wall. These muscles must be mainly responsible for the prominent arching movements of the body as noted in the living specimens. Around the pit the parenchyma is dense and some of its cells are large and glandular.

In the 'tail' region there is a thickening of the normal body musculature, but there are no definite bundles as figured by Wagener (1860) and the present interpretation

agrees with that of Looss (1907). The inversion of the 'tail' during retraction has led to much confusion in the explanation of 'tail' musculature and of excretory system in the Hemiuridae. When the 'tail' is retracted it is also inverted so that the muscles of the body wall which are continuous throughout the tail are reversed around the internal cavity so formed.

The suckers have a typical musculature (Fig. 6) with equatorial, meridional and radial muscles. Some of the equatorial muscles of the oral sucker in this type stand distinct from the remainder of the sucker and appear as two lighter areas on its posterior margin. From them a pair of muscles run posteriorly to be inserted in the ventral body wall one on either side of the pharynx. These areas may possibly be related to the two muscular arches composed of longitudinal and transverse fibres and attached to the posterior rim of the oral sucker. The arches are placed one on either side of the pharynx and probably help in feeding. The ventral sucker has no muscular arches but has a prominent extrinsic musculature inserted in the body wall (Fig. 6). There are seven pairs, one anterior, two antero-lateral, and four postero-dorsal. The anterior pair is very well developed. The most anteriorly situated of the antero-lateral pairs is the more dorsal and runs almost transversely towards the lateral margin. The second pair proceeds almost directly anteriorly. Of the four remaining pairs of postero-laterals, that inserted most anteriorly is the largest and is directed posteriorwards in the centre of the body thickness. The other three postero-laterals are all inserted in the posterior half of the sucker and proceed obliquely anteriorly towards their insertion in the body wall. Of these the most anterior and the most posterior pair are ventrally situated, while the middle pair is dorsal to the first-mentioned postero-lateral.

Digestive system (Figs. 3, 4). The oral aperture communicates directly with the pharynx which lies dorsal and posterior to the oral sucker. It is highly muscular and globular in shape with a diameter of 0·3 mm. It consists mainly of radial fibres bounded towards the parenchyma and towards the cavity by circular and longitudinal muscles, the latter being external. The cavity is lined by cuticle which overlies the musculature.

The pharynx opens posteriorly into a thin-walled sac of irregular shape, lined by cuticle and then circular and longitudinal muscles. This is the oesophagus to which Looss refers as a stomach.

The oesophagus opens laterally, right and left, by a small aperture, bounded by a sphincter muscle, into a globular cavity of greater diameter than the intestine (Fig. 4). Fuhrmann (1928) figured similar cavities for the hemiurid *Distomum ampullaceum* Buttel-Reepen, and gave them the name of gland stomach, and the histological details he gives agrees with the present writer's description of this organ in *Sterrhurus fusiformis* (Fig. 10).

Each gland stomach opens into a long blind unbranched intestinal caecum which proceeds laterally external to the genitalia almost to the 'tail' region (Fig. 3). For most of their course they are dorsal in position becoming more ventral posteriorly. The two caeca approach each other most closely dorsal to the ventral sucker and at their posterior tips. They are lined throughout by numerous columnar epithelial cells, and the muscular coat consists of longitudinal outside circular muscles.

Excretory system (Fig. 3). The excretory aperture at the tip of the 'tail' leads by a sphincter into a medial dorsal unpaired excretory vesicle. This extends in a central position in the body as far as the posterior limits of the testes. Here the vesicle divides into two excretory ducts which diverge widely so that they lie laterally one on either

side of the ventral sucker outside the intestinal caeca and in a dorsal position. They are narrower than the median unpaired vesicle and proceed anteriorly to the level of the posterior edge of the oral sucker where they bend inwards and unite dorsally.

The excretory vesicle is lined by a cellular membrane and contained precipitations of excretory products. Near the distal extremity of the 'tail' the vesicle is larger with more muscular walls and probably functions as a bladder for storage. Inside the 'tail' the vesicle is surrounded by dense glandular parenchyma. When the 'tail' is inverted much of this parenchyma becomes displaced posteriorly so that it surrounds not the vesicle but the cavity formed by the inversion of the 'tail'. Hence some previous writers looked upon this region as a muscular excretory vesicle, while actually the external excretory pore lies at the anterior tip of this new cavity, as noted by Looss (1907).

Nervous system (Figs. 3, 4). A brain was detected consisting of two ganglia situated laterally, one on either side of the pharynx. These ganglia are connected by nerve fibres which encircle the pharynx (Figs. 3, 4). The dorsal commissure is made up entirely of fibres, while in the ventral one numerous deeply stained nerve cells are present. The ganglia are composed of fibres and cells and give rise anteriorly and posteriorly to nerves. The two anterior nerves supply the oral sucker and anterior lip while the posterior pair proceed as ventral cords but were traced only as far as the level of the genital aperture.

Genital system. (1) *Male* (Figs. 3, 4). There are two testes situated ventro-laterally behind the ventral sucker, the left very slightly in advance of the right (Fig. 3). They are longitudinally oval in shape measuring $0{\cdot}33 \times 0{\cdot}29$ mm. From each testis a narrow, straight vas deferens arises in a median antero-dorsal position. The vasa deferentia proceed dorsally in an anterior direction and approach each other above the ventral sucker where they lie on either side of the uterus and internal to the two intestinal caeca. Immediately in front of the ventral sucker the two vasa deferentia open separately into the ventral posterior extremity of the vesicula seminalis. The latter is S-shaped and is not enclosed in a cirrus sac. It is tripartite with a large posterior portion, smaller anterior portion, and a narrow twisted central region. Throughout its course the vesicula seminalis lies dorsal to the corresponding female duct.

The vesicula seminalis opens by a sphincter muscle into a short wide pars prostatica which descends sharply towards the ventral surface (Fig. 4). It is lined by large thin-walled cubical cells. Surrounding the pars prostatica are numerous unicellular prostatic gland cells which are in three ill-defined groups, one dorsal and two ventro-lateral. There is no cirrus sac around the pars prostatica and prostatic gland.

The pars prostatica penetrates a thin muscular sac and passes into the prostatic vesicle lined by a membrane similar to that of the pars prostatica and containing spermatozoa (Fig. 4). Wagener (1860) and Looss (1907) both refer to this sac as a cirrus sac, but, as the latter author observed, it encloses the distal end of the female duct as well as that of the male and is therefore not a true cirrus sac. Manter (1926) refers to it as a sinus sac. The extrinsic muscles of the sac are inserted in the ventral body wall and doubtlessly serve for the protrusion and retraction of the distal ends of the sex ducts in much the same way as a true cirrus functions for the male duct only. The portion of the sac not occupied by the ducts contains loose vacuolated parenchyma cells.

The prostatic vesicle passes into a short narrow ductus ejaculatorius (Fig. 4) which in turn communicates with another longer narrow duct, the 'ductus hermaphroditicus' or genital sinus which opens to the exterior by the common genital pore.

(2) *Female* (Figs. 3, 5). The ovary is situated behind the testes variably to the left or right of the middle line (Fig. 3). It is oval with its long axis transverse and measures 0·33 × 0·42 mm., lying more dorsal than the testes but still in the ventral half of the body. The ova measure 0·006 mm. in diameter. The oviduct arises at the ovicap which is ventro-posterior to the ovary (Fig. 5). It is directed dorsally at first where it receives a short wide duct from the receptaculum seminis, a sac with muscular walls found variably to the right or left of the ovary but always dorsal to the oviduct. The latter now winds ventrally and posteriorly to open into a small ootype, on entering which it receives ventrally the common yolk duct. Surrounding the ootype are numerous unicellular gland cells forming the shell gland with a diameter of 0·14 mm. Around the shell gland and receptaculum seminis are irregular muscle fibres which probably help to press the eggs on into the uterus. Between these muscles and the receptaculum seminis are loose parenchyma cells and much degenerating tissue, probably unwanted sperms. There is no Laürer's canal.

There is one pair of compact vitelline glands consisting of numerous follicles. They are situated close together on the same side of the body as the ovary and ventral to it so that their ducts are very short. They are set obliquely with 3–5 short, blunt, finger-like lobes held together by a broad base. The yolk duct, in each case, arises halfway along the gland and turns dorsally to meet its fellow in a small yolk reservoir immediately beneath the shell gland.

The ootype opens into a thin-walled uterus which is charged with spermatozoa and functions as a receptaculum uterinum. The exact course of the uterus varies with the age of the individual, but it usually proceeds ventral to the female glands and then winds more dorsally on the opposite side of the body between the posterior ends of the intestinal caeca and the ventral sucker (Fig. 3). In this part of its course the uterus is packed with small thin-walled oval eggs measuring 0·018 × 0·009 mm. Posterior to the ventral sucker the uterus passes into the narrower muscular metraterm (Fig. 4) which lies dorsal to the ventral sucker in the middle line. It is lined by cuticle outside which are circular and then longitudinal muscles. It is divided into two sections by a large sphincter muscle immediately anterior to the ventral sucker. The part nearest the uterus is less muscular and is usually filled with eggs, while the distal portion is very narrow and muscular with fewer eggs arranged in one series. Around the metraterm there is dense glandular parenchyma. The tip of the metraterm penetrates the sinus sac which opens confluently with the ductus ejaculatorius into the common genital sinus. Concerning the homologies of this latter various writers have expressed doubt as to whether it represents a part of the uterus, part of the ejaculatory duct or an invagination of the body wall as in the genital cloaca of other trematodes.

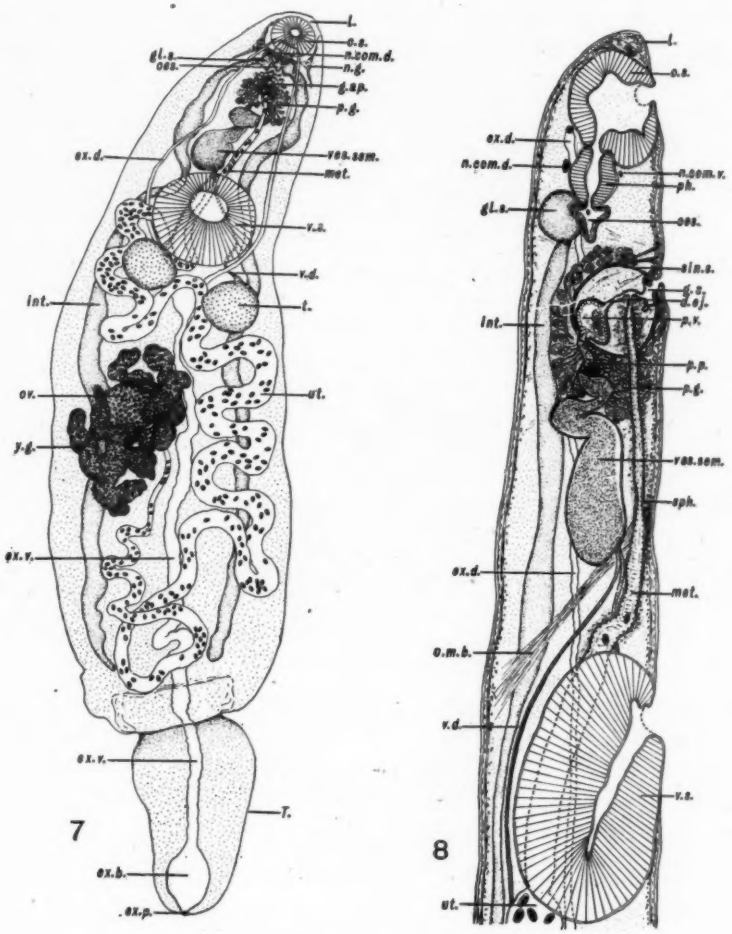
Sterrhurus fusiformis (Lühe, 1901) (Figs. 7, 8, 10, 11)

Synonymy. 1901. *Lecithochirium fusiforme* Lühe.
1907. *Sterrhurus fusiformis* (Lühe).

The descriptions of this parasite which are so far published are those of Lühe (1901), Looss (1907), Linton (1910) and Mathias (1934). None of these is complete, while Linton's account of the excretory vesicle is incorrect.

External features (Fig. 7). *Sterrhurus fusiformis* can be distinguished from *Lecithochirium rufoviride* by its more slender body, pointed anterior end, longer 'tail', deep

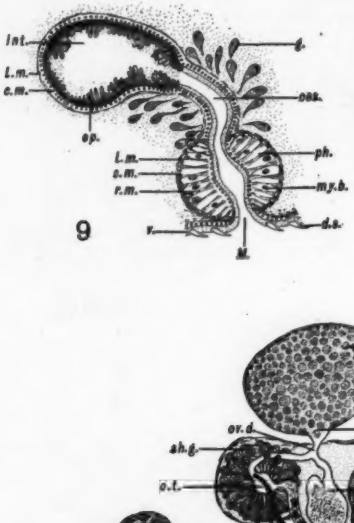
brown eggs, simple and smaller oral sucker, a very small anterior lip, and the absence of a preacetabular pit. As in *L. rufoviride* the body is cylindrical, thick and very muscular, and with a smooth cuticle. It measures 5 × 1·7 mm., the 'tail' making up almost half the total body length in the living specimen but undergoing more contraction than any other part of the body on fixation.

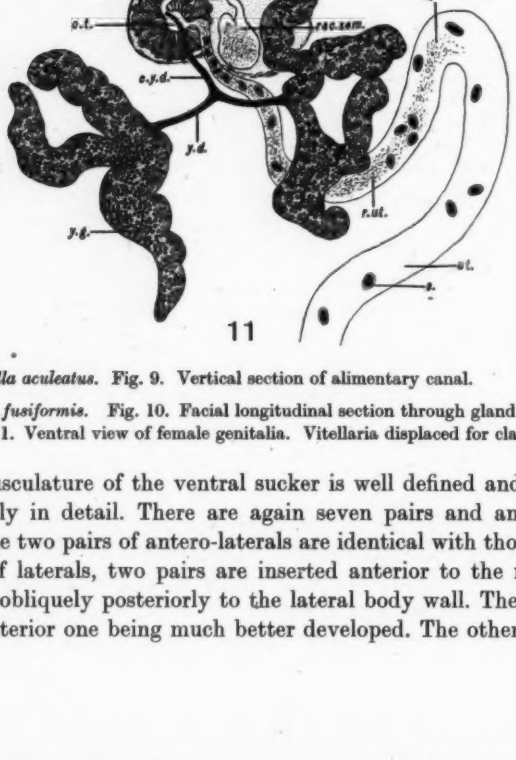


Sterrhurus fusiformis. Fig. 7. General anatomy from ventral surface.
Fig. 8. Left anterior sector of body viewed from centre.

The oral sucker measures 0·28 mm. in diameter, and the ventral sucker, separated from it by a third of the length of the body, has a diameter of 0·60 mm. Both suckers are circular and the ratio of oral to ventral is 1 : 2. The anterior lip is hardly visible in the whole mount and there is no preacetabular pit. The genital and excretory pores occupy the same positions as in *L. rufoviride*.

Muscular system. The musculature of the body wall, ventral suckers and 'tail' region is the same as that previously described for *L. rufoviride*. The oral sucker in *Sterrhurus fusiformis* has no muscular arches, but the pair of lateral muscle bands originating in the postero-lateral border of the oral sucker and inserted in the ventral body wall are very prominent. The muscles of the preoral lip are feebly developed compared with *L. rufoviride*, but although there is no preacetabular pit the diagonal muscles developed in relation to it are well developed (Fig. 8).





Skrjabiniella aculeatus. Fig. 9. Vertical section of alimentary canal.

Sterrhurus fusiformis. Fig. 10. Facial longitudinal section through gland stomach.
Fig. 11. Ventral view of female genitalia. Vitellaria displaced for clarity.

The extrinsic musculature of the ventral sucker is well defined and differs from that of *L. rufoviride* only in detail. There are again seven pairs and an additional single anterior bundle. The two pairs of antero-laterals are identical with those in *L. rufoviride*. Of the five pairs of laterals, two pairs are inserted anterior to the middle line of the sucker and extend obliquely posteriorly to the lateral body wall. These are both dorsal in position, the posterior one being much better developed. The other three laterals are

all ventral in position and inserted in the posterior half of the sucker and extend obliquely forwards at varying angles to their insertions in the musculature of the body wall. Beneath the body musculature there are again glandular cells in the parenchyma especially in the region of the lip and in a ventral position between the two suckers.

Digestive system (Figs. 7, 8, 10). The anatomy is identical with that described for *L. rufoviride*. Here, in addition, regurgitation movements were watched under the coverslip in the living animal, and this enabled the writer to make out more of the detailed histology of the gland stomach than in the previous type (Fig. 10). At either end of the gland stomach towards the oesophagus and the intestine are sphincter muscles. It also has a large sphincter in its wall which contracts when the cavity is full, sending food either into the intestine as in feeding or into the oesophagus as in regurgitation. From the oesophagus the unwanted food is passed out by the backward contraction of the pharyngeal bulb. The muscular walls of the gland stomach between the oesophagus and the gland stomach sphincter are lined by regular epithelial cells. These probably secrete mucin, since the contents of the gland stomach always take up the stain less readily than other parts of the digestive system. The mucus probably binds particles together either for the food stream or for regurgitation. The second half of the gland stomach beyond the sphincter is lined by very pronounced ciliated epithelium which obviously aids the passage of food into the intestine.

Excretory and nervous systems (Figs. 7, 8). These systems, so far as they were worked out, are practically identical with the corresponding structures in *L. rufoviride* except for the greater thickening of the muscular walls of the distal part of the excretory vesicle.

Genital system. (1) *Male* (Figs. 7, 8). The general arrangement resembles closely that of *L. rufoviride*. This type can be distinguished, however, by the transversely oval shape of the testes which measure $0{\cdot}25 \times 0{\cdot}31$ mm. The pars prostatica is shorter here than in the previous type and the sinus sac is larger with more clearly defined walls. The comparatively larger size of the vesicula seminalis without a definite neck region, and the more extensive prostate gland in *Sterrhurus fusiformis* indicate only that the worms investigated were in a different phase of development from the specimens of *Lecithochirium rufoviride*.

(2) *Female* (Fig. 11). The arrangement is again similar to that in *L. rufoviride*. The ovary is transversely oval measuring $0{\cdot}33 \times 0{\cdot}37$ mm. lying in a similar position to that in the previous type. The ova are round and have a diameter of 0·008 mm., while the ripe eggs are only slightly longer than broad and measure $0{\cdot}024 \times 0{\cdot}018$ mm., being larger than in *L. rufoviride* and of a deeper brown colour. The vitelline glands, again obliquely placed, have more slender lobes with a more slender basal connecting region. In the specimens figured the female glands were on the right side of the body, but again the position seems to be variable. In connexion with this reversal to the right side, the receptaculum seminis is to the left of the shell gland and the main coils of the uterus are on the left instead of the right.

DISCUSSION ON HEMIURID WORMS

Lühe (1901) defined the genus *Lecithochirium* as Hemiuridae with ventral 'cervical groove' or preacetabular pit, oral sucker with a lip, thick body, 'tail' not invaded by uterus or alimentary canal, 'cirrus sac' not well defined, S-shaped vesicula seminalis in front of ventral sucker, yolk glands small and spread out like a hand. He distinguished the

type-species *L. rufoviride* by its large oral sucker, bluntly pointed forebody, ratio of oral to ventral suckers, two muscular hemispherical arches on the inner surface of oral sucker and one on either side of pharynx, large preacetabular pit resembling an accessory sucker, and thick yolk glands with free ends club-shaped. *L. fusiforme* (=*Sterrhurus fusiformis*) he distinguished from the former species by its slender spindle-shaped body with pointed anterior end, by the form of the yolk glands with more slender, longer lobes, and the large 'tail' invaded by uterus and caeca.

Looss (1907) created the subfamily Sterrhurinae which included the whole of Lühe's genus *Lecithochirium* and some additional genera. He redefined the genus *Lecithochirium* s.str. as forms with an oral sucker with two muscular hemispherical arches on its inner ventral wall and with a transversely elongate aperture, a highly muscular lip, and deep preacetabular pit. He created the new genus *Sterrhurus* which gives its name to the subfamily and includes *S. fusiformis*. The genus *Sterrhurus* he defined as forms with oral sucker round and without appendages, pre-oral lip only slightly muscular, preacetabular pit small or missing, eggs rounded and only slightly longer than broad.

Looss's classification holds good in the main for all the types he described but there is confusion with regard to the new species added to both genera since 1907. Thus with regard to the muscular hemispherical arches in the oral sucker, these are absent not only in the genus *Sterrhurus* but also in five new species of the genus *Lecithochirium*. In addition, the variation in the development of the preacetabular pit seems to be one merely of degree as the genus *Lecithochirium* has *L. gravidium* Looss, *L. synodi* Manter, and *L. exodicum* McFarlane with small pits while in the genus *Sterrhurus*, *S. monticelli* (Linton) is described as possessing a definite preacetabular pit. Furthermore, *S. fusiformis* described in this paper, although possessing no definite pit has the pair of oblique muscles in the same position and as well developed as in *Lecithochirium rufoviride*, while other writers have noted the pit in many Digenea other than the Hemiuridae. The nature of the pre-oral lip seems again to be only a difference of degree; in the genus *Sterrhurus* there is *S. robustus* Manter with a very definite lip while in the genus *Lecithochirium*, *L. copulans* (v. Linst.), *L. gravidium* Looss, *L. dillanei* Nicoll, *L. synodi* Manter, and *L. microstomum* Chandler are described as possessing very small lips. So far as present data indicates it does not seem possible, either, to divide these two genera on shape or size of egg: these, as well as 'tail' length, sucker ratio, shape of sinus sac and yolk glands seem to be features of no more than specific value. Therefore the separation of the two genera *Lecithochirium* and *Sterrhurus* is very tentative. According to present classification, *Sterrhurus* is defined entirely on negative features which are really only differences of degree. Further descriptive work on the species of these two genera will be necessary before they can be redefined.

Summary

1. The anatomy of three digenetic trematodes from *Conger conger* (Linn.), *Skrjabiniella aculeatus* (Odhner), *Lecithochirium rufoviride* (Rud.) and *Sterrhurus fusiformis* (Lühe) has been described. The technique employed is given, and in each case the history of the species has been traced.

2. The discussion on the nomenclature of *Skrjabiniella aculeatus* explains why this generic name used by Issaitschikow (1928) has been adopted in this work in place of

Prosorhynchus, and a key to the genera *Prosorhynchus* s.str. and *Skrjabiniella* has been suggested. A table showing the proposed division of Odhner's genus *Prosorhynchus* is included.

3. In the discussion on the hemiurid worms it is pointed out that there is no sound basis for the separation of the genera *Lecithochirium* and *Sterrhurus* as they stand.

Key to lettering. *a.* muscular arch; *b.w.* body wall; *c.* cuticle; *cil.* cilia; *cir.s.* cirrus sac; *c.m.* circular muscles; *c.y.d.* common yolk duct; *d.ej.* ductus ejaculatorius; *d.s.* dermal spines; *d.v.m.* dorso-ventral muscles; *e.* egg; *e.m.* equatorial muscles; *ep.* epithelium; *ex.b.* excretory bladder. *ex.d.* excretory duct; *ex.p.* excretory pore; *ex.v.* excretory vesicle; *g.* gland cell; *G.* 'genital tongue'; *g.ap.* genital aperture; *g.s.* genital sinus; *gl.s.* gland stomach; *int.* intestine; *l.* lip; *Lc.* Laürer's canal; *l.m.* longitudinal muscles; *M.* mouth; *m.b.* muscle bundle; *met.* metraterm; *myb.* myoblast; *n.comm.d.* dorsal nerve commissure; *n.comm.v.* ventral nerve commissure; *n.g.* nerve ganglion; *oes.* oesophagus; *o.m.* oblique muscles; *o.m.b.* oblique muscle bundle; *o.s.* oral sucker; *o.t.* ootype; *ov.* ovary; *ov.c.* ovicap; *ov.d.* oviduct; *p.g.* prostatic gland cell; *ph.* pharynx; *p.p.* pars prostatica; *pr.* preacetabular pit; *p.v.* prostatic vesicle; *rec.sem.* receptaculum seminis; *rh.* rhynchus; *r.m.* radial muscles; *r.ut.* receptaculum uterinum; *sh.* 'shoulder'; *sh.g.* shell gland; *sin.s.* sinus sac; *s.m.* sucker muscle; *sp.* spermatozoa; *sph.* sphincter; *t.* testis; *T.* 'tail'; *ut.* uterus; *v.* ventral surface; *v.d.* vas deferens; *ves.sem.* vesicula seminalis; *v.s.* ventral sucker; *y.d.* yolk duct; *y.g.* yolk gland; *y.res.* yolk reservoir.

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GENERA AND SPECIES OF PARASITIC MITES (ACARINA)

By CHARLES D. RADFORD, F.Z.S.*

Introduction

During my work on the mites I have often wished that a book were available in which all the known and valid genera and species of parasitic mites could be found. The literature on the Acarina contains numerous genera and species which are synonyms of older identifications.

It is hoped that the present paper will in some small way assist my fellow-acarologists as a reference work and eliminate the tendency to duplicate the work of others and cause a glut of synonyms. I have attempted to give herein the genera, species, authority, year of validity and, where possible, the original host.

The list of references is not exhaustive, my endeavour being to list only those papers in which the original descriptions have appeared. An asterisk placed before the author's name signifies that the paper is in the library of the Zoological Society of London, papers in the possession of the author are marked with an obelisk.

I am indebted to Mr G. B. Stratton, Librarian of the Zoological Society, for the very valuable assistance which he has given in helping me to trace most of the papers used in the compilation of this paper. Also to Mr G. Wilson, Librarian, Manchester Medical Society, for facilities in the Library.

The nomenclature of hosts has been checked at the British Museum (Nat. Hist.), and I am indebted to Mr M. A. C. Hinton and staff for their help. The nomenclature of rodents is that published by the British Museum (Nat. Hist.), in *Families and Genera of Living Rodents*, 2 vols., by J. R. Ellerman.

Kolenati (1858) raised the genus *Steatonyssus* for those mites of the family Liponyssidae in which the dorsum is covered by two dorsal scutae. Ewing (1922) raised the genus *Ceratonyssus* for those mites possessing two dorsal scutae. Willman (1936) pointed out that Ewing's genus was a synonym of Kolenati's genus and therefore *Steatonyssus* was valid having priority over *Ceratonyssus*.

The species *ceratognathus* Ewing, 1922 and *occidentalis* Ewing, 1933 are therefore included in the genus *Steatonyssus* Kolenati, 1858.

The genus *Tertragonyssus* Ewing, 1922 appears to be synonymous with *Laelaps* Koch, 1842. The type species of *Tetragonyssus* is *T. gigas* Oudemans, 1912, which is proper to the genus *Myonyssus* Tiraboschi, 1904. Ewing (1933) states that his genus is 'very near *Myonyssus* Tiraboschi, 1904'. The other species placed in the genus by Ewing (1922), i.e. *Tetragonyssus spiniger* Ewing & Stover and *T. bermudaensis* Ewing, are, from the author's description, more appropriate to the genus *Laelaps* Koch, 1842. They conform to the generic description of *Laelaps* and possess on the dorsal surface of femur I the group of long spines. The species *spiniger* Ewing & Stover taken on the muskrat is identical to *Laelaps multispinosus* Banks, 1909 and must be considered a synonym.

From the descriptions of *Tetragonyssus bermudaensis* Ewing, 1922 and *T. microti* Ewing, 1933 it would appear that these should also be placed in the genus *Laelaps* Koch, 1842.

* Work carried out with the aid of a Government Grant.

Banks (1910) briefly described and figured a mite to which he gave the name *Laelaps longitarsus*. The figures are of half the specimen, i.e. divided down the centre of the body from capitulum to posterior tip of body. Banks's fig. 30 shows no spines on the sternal, genito-ventral or anal scutae. It is therefore difficult to place the specimen, but from the figure it appears that there is a triangular scutum posterior to leg iv. This, together with the shape of the ventral scutae and the numerous spines on the dorsal scutum (depicted in Banks's fig. 24) suggests the mite should be placed in the genus *Eulaelaps* Berlese, 1903*b*.

In the same paper (Banks, 1910) two other mites are briefly described and very inadequately figured. Banks's fig. 4 shows the half-dorsum of *Pteropus echinipes* and fig. 14 that of *P. grossus*. The genus *Pteropus* (Pteroptus) is a synonym of *Spinturnix* von Heyden, and Banks's specimens, would, in normal circumstances, be renamed *Spinturnix echinipes* and *S. grossus*. As the ventral scutae are neither figured nor described it is not possible to establish the validity of these species, which should therefore remain as doubtful.

Genus **Laelaps** Koch, 1842

Laelaps muris Ljungh, 1799	*Arvicola amphibius amphibius* L., 1758
L. pachypus Koch, 1839	*Microtus arvalis arvalis* Pallas, 1778
L. lemni Grube, 1851	*Lemmus obensis obensis* Brants, 1827
L. echidninus Berlese, 1887	*Rattus norvegicus norvegicus* Berkenhout, 1769
L. multispinosus Banks, 1909	*Ondatra zibethica zibethica* L., 1766
L. wolffsohni Oudemans, 1910	—
L. rothschildi Hirst, 1914	*Melomys rufescens rufescens* Alston, 1872
L. nuttalli Hirst, 1915	*Rattus rattus rattus* L., 1758
L. arvicolae Oudemans, 1916	*Microtus arvalis arvalis* Pallas, 1778
L. bermudaensis Ewing, 1922	Wood rat
L. parvulus Hirst, 1923	*Lemniscomys griselda spinalis* Thomas, 1916
L. vansomereni Hirst, 1923	*Aethomys chrysophilus chrysophilus* de Winton, 1896
L. hawaiiensis Ewing, 1924	*Rattus hawaiiensis* Stone, 1917
L. algericus Hirst, 1925	*Mus musculus algirus* Pomel, 1856
L. aethiopicus Hirst, 1925	Rats
L. lamborni Hirst, 1925	Rats
L. liberiensis Hirst, 1925	*Dephomys defua* Miller, 1900
L. oraniensis Hirst, 1925	Field mice
L. soricis Oudemans, 1925	*Sorex*
L. hollisteri Ewing, 1925	*Peromyscus californicus californicus* Gambel, 1848
L. barbatus Ewing, 1925	Lemur
L. braziliensis Ewing, 1925	*Galea spixii* Wagler, 1831
L. wetmorei Ewing, 1925	Rat
L. robustipes Ewing, 1925	Rodent
L. californicus Ewing, 1925	?
L. glasgowi Ewing, 1925	Wild rat
L. virginianus Ewing, 1925	Wild mouse

Laelaps reithrodontis Ewing, 1925	*Reithrodon cuniculoides cuniculoides* Waterhouse, 1837
L. hilaroides Oudemans, 1928	*Eptesecus serotinus* Schreber
L. cancer Pearse, 1929	*Gecarcinus lateralis* Freminville
L. jettmari Vitzthum, 1930	*Apodemus agrarius agrarius* Pallas, 1778
L. pallidus Tragardh, 1931	—
L. hapoloti Hirst, 1931	*Hapolotis*
L. microti Ewing, 1933	*Microtus californicus*
L. paulistanensis Fonseca, 1935	White rat
L. manquinhosi Fonseca, 1935	*Holochilus vulpinus* Lichtenstein, 1827
L. differens Fonseca, 1935	Wild rat
L. exceptionalis Fonseca, 1935	Wild rat
L. lativentralis Fonseca, 1935	Wild rat
L. finlaysoni Womersley, 1937	*Gyomys apodemoides* Finlayson, 1932
L. melomys Womersley, 1937	*Melomys cervinipes littoralis* Lönneberg, 1916
L. berlesei Fonseca, 1938	*Gallictis vittata*
L. thori Fonseca, 1938	?
L. aragonensis Fonseca, 1938	Rats
L. navasi Fonseca, 1938	*Oryzomys eliurus* Wagner, 1845
L. hirsti Fonseca, 1938	*Oryzomys eliurus* Wagner, 1845
L. mazzi Fonseca, 1938	Rats
L. buxtoni Radford, 1941	Gerbille

Genus **Gigantolaelaps** Fonseca, 1938

Gigantolaelaps maximus Berlese, 1903	*Oryzomys subflavus* Wagner, 1842
G. versteegi Oudemans, 1904	*Mus* sp.
G. brachyspinosus Fonseca, 1935	*Holochilus vulpinus* Lichtenstein, 1827
G. butantanensis Fonseca, 1935	*Oryzomys eliurus* Wagner, 1845
G. mattogrossensis Fonseca, 1935	*Holochilus vulpinus* Lichtenstein, 1827
G. goyanensis Fonseca, 1938	*Estrimys* sp.
G. comatus Fonseca, 1938	Field rat
G. vitzthumi Fonseca, 1938	Wild rat
G. oudemansi Fonseca, 1938	Wild rat
G. gilmorei Fonseca, 1938	Rats

Genus **Macrolaelaps** Ewing, 1929

Macrolaelaps muricola Tragardh, 1908	*Mastomys coucha hildebrandti* Peters, 1878
M. giganteus Berlese, 1918	*Lemniscomys griselda spinalis* Thomas, 1916
M. ugandanus Hirst, 1923	Rodent
M. bakeri Hirst, 1923	*Rhabdomys pumilio pumilio* Sparrmann, 1784
M. grandis Hirst, 1923	Rat
M. sanguisugus Vitzthum, 1926	*Akodon olivaceus* Waterhouse, 1837
M. sculpturatus Vitzthum, 1926	*Rattus whiteheadi whiteheadi* Thomas, 1894

Genus **Eulaelaps** Berlese, 1903

Eulaelaps stabularis Koch, 1836	*Talpa europaea* L.
E. oribatoides Michael, 1892	*Talpa europaea* L.

Eulaelaps pontiger Berlese, 1903	Rat
E. propheticus Banks, 1909	Groundhog
E. pedalis Banks, 1909	Chipmunk
E. novus Vitzthum, 1924	*Riparia riparia* L.
E. cricetuli Vitzthum, 1930	*Phodopus roborovskii bedfordiae* Thomas, 1908
E. vitzthumi Fonseca, 1935	Wild rat
E. citellus Radford, 1942	*Citellus beecheyi beecheyi* Richardson, 1829

Genus **Androlaelaps** Berlese, 1903

Androlaelaps hermaphrodita Berlese, 1887	—
A. karawaiewi Berlese, 1903	*Formica pratensis*
A. sardous Berlese, 1911	*Apodemus sylvaticus sylvaticus* L., 1758
A. marshalli Berlese, 1911	Rats

Genus **Haemolaelaps** Berlese, 1910

Haemolaelaps marsupialis Berlese, 1910	*Perameles*
H. centrocarpus Berlese, 1911	Rats
H. inops Berlese, 1911	Rats
H. fahrenholzi Berlese, 1911	*Apodemus sylvaticus sylvaticus* L., 1758
H. murinus Berlese, 1911	Rats
H. capensis Hirst, 1916	*Cryptomys hottentotus hottentotus* Lesson, 1826
H. callosus Berlese, 1917	*Lophuromys aquilus zena* Dollman, 1909
H. phialiger Berlese, 1917	*Acromyrmex lundi*
H. villosissimus Berlese, 1918	*Saccostomus campestris campestris* Peters, 1846
H. spinitarsus Berlese, 1918	*Georychus* sp.
H. scapularis Berlese, 1918	*Spalax microphthalmus* Guldenstaedt, 1770
H. inops var. *zulu* Berlese, 1918	*Lemniscomys griselda spinalis* Thomas, 1916
H. elongatus Berlese, 1918	Detritus
H. concurrens Berlese, 1918	Muscis
H. inversus Berlese, 1918	Detritus
H. spinosulus Berlese, 1921	—
H. subterraneus Berlese, 1921	—
H. mauritanicus Hirst, 1925	*Gerbillus*
H. mohrae Oudemans, 1925	*Microtus arvalis arvalis* Pallas, 1778
H. omnitectus Vitzthum, 1928	*Chrysocolaptes validus* Temminck
H. molestus Oudemans, 1929	—
H. tachyoryctes Radford, 1941	*Tachyoryctes ruddi ruddi* Thomas, 1909
H. mesopicos Radford, 1942	*Mesopicos ruwenzorii* Sharpe
H. mystromys Radford, 1942	*Mystromys albicaudatus albicaudatus* Smith, 1834

Genus **Neolaelaps** Hirst, 1926

Neolaelaps magnistigmatus Vitzthum, 1918	*Pteropus edulis* Geoffroy
N. echinus Oudemans, 1925	Bat

Genus **Heterolaelaps** Hirst, 1926

Heterolaelaps antipodianum Hirst, 1926	*Perameles nasuta*

Genus **Mesolaelaps** Hirst, 1926

Mesolaelaps anomalus Hirst, 1926	*Perameles*
M. australiensis Hirst, 1926	Mice
M. lagotisinus Hirst, 1931	*Thalacomys lagotis* Reid

Genus **Tricholaelaps** Vitzthum, 1926

Tricholaelaps comatus Vitzthum, 1926	*Rattus whiteheadi whiteheadi* Thomas, 1894

Genus **Longolaelaps** Vitzthum, 1926

Longolaelaps longulus Vitzthum, 1926	*Rattus whiteheadi whiteheadi* Thomas, 1894

Genus **Neoparalaelaps** Fonseca, 1935

Neoparalaelaps bispinosus Fonseca, 1935	*Cavia aperea aperea* Erxleben, 1777

Genus **Eubrachylaelaps** Fonseca, 1935

Eubrachylaelaps rotundus Fonseca, 1935	Wild rat

Genus **Cavilaelaps** Fonseca, 1935

Cavilaelaps bresslaui Fonseca, 1935	*Caviella australis australis* Geoffroy, 1833

Genus **Mysolaelaps** Fonseca, 1935

Mysolaelaps parvispinosus Fonseca, 1935	Rat
M. microspinosus Fonseca, 1935	Rat

Genus **Ischnolaelaps** Fonseca, 1935

Ischnolaelaps reticulatus Fonseca, 1935	*Euryzygomatomys spinosus catellus* Thomas, 1916
I. coelogenys Fonseca, 1935	*Cuniculus paca paca* L., 1766
I. sciureus Fonseca, 1935	*Sciureus aestuans aestuans* L., 1766
I. dasymys Radford, 1939	*Dasymys incomtus helukus* Heller, 1910
I. arvicanthis Radford, 1939	*Arvicanthis abyssinicus rubescens* Wroughton, 1909
I. tateronis Radford, 1939	*Tatera benvenuta benvenuta* Hinton & Kershaw, 1920
I. cryptomius Radford, 1939	*Georychus capensis capensis* Pallas, 1779
I. rhabdomys Radford, 1939	*Rhabdomys pumilio pumilio* Sparrmann, 1784
I. bathyergus Radford, 1939	*Bathyergus suillus suillus* Schreber, 1782

Genus **Cyclolaelaps** Ewing, 1933

Cyclolaelaps circularis Ewing, 1933	*Peromyscus truei truei* Shufeldt, 1886
C. lophuromius Radford, 1939	*Lophuromys aquilus aquilus* True, 1892

Genus **Hemilaelaps** Ewing, 1933

Hemilaelaps americanus Ewing, 1933	*Drymarchon corais melanurus*
H. distinctus Ewing, 1933	*Elaphe obsoleta*

Genus **Spinolaelaps** Radford, 1940

Spinolaelaps jacksoni Radford, 1940	*Rhinolophus lobatus* Peters

Genus **Myonyssus** Tiraboschi, 1904

Myonyssus decumani Tiraboschi, 1904	*Rattus norvegicus norvegicus* Berkenhout, 1769
M. gigas Oudemans, 1912	Mole nest

Genus **Myonyssoides** Hirst, 1925

Myonyssoides capensis Hirst, 1925	*Cryptomys hottentotus hottentotus* Lesson, 1826

Genus **Mungosicola** Radford, 1942

Mungosicola ugandae Radford, 1942	*Mungos mungo macrurus* Thomas

Genus **Ugandolaelaps** Radford, 1942

Ugandolaelaps protoxera Radford, 1942	*Protoxerus stangeri centricola* Thomas, 1906

Genus **Ligialaelaps** Radford, 1942

Ligialaelaps ewingi Pearse, 1930	*Ligia exotica* Roux

Genus **Banksia** Radford, 1942

Banksia longiseta Banks, 1909	Carrion beetle

Genus **Haemogamasus** Berlese, 1889

Haemogamasus hirsutus Berlese, 1889	*Talpa europaea* L.
H. nidi Michael, 1892	*T. europaea* L.
H. horridus Michael, 1892	*Apodemus sylvaticus sylvaticus* L., 1758
H. oudemansi Hirst, 1914	*Rattus norvegicus norvegicus* Berkenhout, 1769
H. liberiensis Hirst, 1916	*Hylomys trivirgatus trivirgatus* Temminck, 1853
H. horridus var. *arvicolarum* Berlese, 1920	*Microtus arvalis arvalis* Pallas, 1778
H. sanguineus Ewing & Stover, 1924	—
H. alaskensis Ewing, 1925	*Microtus* sp.
H. liponyssoides Ewing, 1925	*Scalops argentatus*
H. reidi Ewing, 1925	*Sciurus* sp.
H. barberi Ewing, 1925	?
H. microti Ewing, 1925	*Microtus* sp.
H. twitchelli Ewing, 1925	*Clethrionomys dawsoni dawsoni* Merriam, 1888
H. quadrisetatus Vitzthum, 1926	*Akodon olivaceus* Waterhouse, 1837
H. mandschuricus Vitzthum, 1930	*Phodopus roborovskii bedfordiae* Thomas, 1908
H. avisugus Vitzthum, 1930	*Riparia riparia* L.
H. sternalis Ewing, 1933	*Blarina brevicauda talpoides*

Genus **Euhaemogamasus** Ewing, 1933

Euhaemogamasus onychomydis Ewing, 1933	*Onychomys* sp.
E. oregonensis Ewing, 1933	*Phenacomys albipes* Merriam, 1901
E. utahensis Ewing, 1933	*Neotoma lepida lepida* Thomas, 1893

Genus **Raillietia** Trouessart, 1902

Raillietia auris Leidy, 1872	Ox
R. hopkinsi Radford, 1938	*Kobus defassa ugandae* Neumann

Genus **Manisicola** Lawrence, 1939

Manisicola africana Lawrence, 1939	*Smutsia temminckii* Smuts

Genus **Ewingia** Pearse, 1929

Ewingia cenobitae Pearse, 1929	*Cenobita diogenes* Latreille

Genus **Echinonyssus** Hirst, 1925

Echinonyssus nasutus Hirst, 1925	*Tupaia picta*

Genus **Liponyssus** Kolenati, 1858

Liponyssus decussatus Kolenati, 1857	*Myotis dasycnemus* Boie
L. ellipticus Kolenati, 1857	—
L. flavus Kolenati, 1857	*Nyctalus noctula* Daubenton
L. fossulatus Kolenati, 1857	*Myotis daubentonii* Kuhl
L. granulosus Kolenati, 1857	*Miniopterus schreibersi* Kuhl
L. longimanus Kolenati, 1857	*Rousettus aegyptiaca* Geoffroy
L. setosus Kolenati, 1857	*Rhinolophus euryale* Blasius
L. sylviarum Canestrini & Fanzago, 1877	—
L. uncinatus Canestrini, 1885	*Rhinolophus euryale* Blasius
L. bursa Berlese, 1888	*Gallus domesticus*
L. lacertinus Berlese, 1892	*Lacerta viridis*
L. saurarum Oudemans, 1901	*Lacerta agilis* L.
L. blanchardi Trouessart, 1904	Marmot
L. americanus Banks, 1905	*Peromyscus eremicus eremicus* Baird, 1857
L. cyclaspis Oudemans, 1906	*Pipistrellus pipistrellus* Schreber
L. canadensis Banks, 1909	*Passer domesticus* L.
L. liberiensis Hirst, 1912	Squirrel
L. creightoni Hirst, 1912	Porcupine
L. bacoti Hirst, 1913	*Rattus norvegicus norvegicus* Berkenhout, 1769
L. piger Berlese, 1918	Snake
L. sternalis Hirst, 1921	Bat
L. sciurinus Hirst, 1921	Squirrel
L. aethiopicus Hirst, 1921	Elephant shrew
L. confuscianus Hirst, 1921	*Myospalax cansus cansus* Lyon, 1907
L. macedonicus Hirst, 1921	*Spalax monticola thermaicus* Hinton, 1920
L. tenuiscutatus Ewing, 1922	Sweet potatoes
L. pacificus Ewing, 1922	Brewer's blackbird
L. crosbyi Ewing	*Vesper subulatus*
L. constrictus Ewing, 1922	Wood thrush
L. montanus Ewing, 1922	*Tamiasciurus hudsonicus richardsoni* Bachman, 1838
L. triangulus Ewing, 1922	*Lampropeltis calligaster*

Liponissus occidentalis Ewing, 1922	*Tamiasciurus hudsonicus richardsoni* Bachman, 1838
L. gordonensis Hirst, 1923	*Mabuia quinquestriata* Lichtenstein
L. monodi Hirst, 1925	*Acanthodactylus*
L. heterotarsus Vitzthum, 1925	—
L. brevipes Ewing, 1925	*Piranga erythromelas*
L. robustipes Ewing, 1925	*Tadarida mexicana* Saussure
L. chilensis Ewing, 1925	*Tadarida brasiliensis* Geoffroy
L. corethroproctus Oudemans, 1902	*Myotis dasycnemus* Boie
L. nagayoi Yamada, 1931	Man and rat
L. venezolanus Vitzthum, 1931	*Molossos nasutus* Spix
L. eruditis Fonseca, 1935	Found on laboratory table
L. hirsti Fonseca, 1935	*Caviella australis australis* Geoffroy & D'Orbigny, 1833
L. haematophagus Fonseca, 1935	Bat
L. iheringi Fonseca, 1935	*Donacobius atricapillus* L.
L. pereirai Fonseca, 1935	Wild rat
L. wernecki Fonseca, 1935	*Didelphys aurita* Wied
L. brasiliensis Fonseca, 1938	*Cavia aperea aperea* Erxleben, 1777
L. nyctinomius Radford, 1938	*Nyctinomus brasiliensis* Geoffroy
L. britannicus Radford, 1941	*Nyctalus noctula* Schreber
L. cynomys Radford, 1941	*Cynomys* sp.
L. otomys Radford, 1942	*Otomys* sp.
L. sangsteri Radford, 1942	*Protoxerus stangeri centricola* Thomas, 1906

Genus **Liponysella** Hirst, 1925

Liponysella madagascariensis Hirst, 1921	*Lemur mongox* var. *albifrons*

Genus **Ophionyssus** Megnin, 1884

Ophionyssus natricis Gervais, 1844	*Coluber viridiflavus*
O. serpentium Hirst, 1915	*Thamnophis ordinoides ordinoides* B. & G.
O. easti Ewing, 1925	*Sceloporus graciosus*

Genus **Steatonyssus** Kolenati, 1858

Steatonyssus musculi Schrank, 1803	—
S. vespertilionis Duges, 1834	—
S. javensis Oudemans, 1914	Bat
S. biscutatus Hirst, 1921	*Dendropicus cardinalis*
S. nyassae Hirst, 1921	Elephant shrew
S. viator Hirst, 1921	*Cypselus affinis*
S. arabicus Hirst, 1921	*Agama adramitana*
S. ceratognathus Ewing, 1922	*Nycticeius humeralis* Rafinesque
S. sudanensis Hirst, 1926	*Liponycteris nudiventris* Cretzschmar
S. occidentalis Ewing, 1933	*Myotis* sp.
S. joaquimi Fonseca, 1935	*Glossophaga soricina* Pallas
S. spinosus Willman, 1936	*Solenodon paradoxus* Brdt.

Genus **Ichoronyssus** Kolenati, 1858

Ichoronyssus arcuatus Koch, 1839	*Nyctalus noctula* Schreber
I. carnifex Koch, 1839	*Vespertilio* sp.
I. albatus Koch, 1839	—
I. scutatus Kolenati, 1857	*Rhinolophus ferrum equinum* Daubenton
I. semitectus Koch	—
I. isabellinus Oudemans, 1913	*Putorius* sp.
I. diversipilis Vitzthum, 1918	*Vesperugo pipistrella*
I. sternalis Ewing, 1922	Woodchuck
I. spinosus Oudemans	—
I. hasei Vitzthum, 1931	Bat
I. mohrae Vitzthum, 1931	*Vespertilio nattereri* Kuhl
I. butantanensis Fonseca, 1932	White mouse

Genus **Dermanyssus** Duges, 1834

Dermanyssus gallinae Redi, 1674	*Gallus domesticus*
D. hirundinis Herman, 1804	—
D. avium Duges, 1834	—
D. muris Hirst, 1913	*Rattus rattus rattus* L., 1758
D. aegyptius Hirst, 1913	*Acomys cahirinus* Desmarest, 1819
D. sanguineus Hirst, 1914	*Rattus rattus rattus* L., 1758
D. quintus Vitzthum, 1920	*Dendrocopus major*
D. americanus Ewing, 1922	*Passer domesticus* L.
D. oti Ewing, 1925	*Otus asio asio*
D. murinus Oudemans, 1929	*Rattus rattus* var.
D. evotomydis Ewing, 1933	*Evotomys* sp.
D. prognephilus Ewing, 1933	*Progne subis subis*
D. brasiliensis Fonseca, 1935	*Holochilus sciureus* Wagner, 1842
D. brevis Ewing, 1936	*Otocoris alpestris merrilli*
D. scutatus Ewing, 1936	*Colaptes cafer cafer*
D. chelidonis Oudemans, 1939	—

Genus **Spinturnix** von Heyden, 1826

Spinturnix vespertilionis L., 1758	*Myotis myotis* Borkhausen
S. acuminatus Koch, 1836	*Nyctalus noctula* Schreber
S. plecotinus Koch, 1836	—
S. murinus Walkenaer, 1847	—
S. psi Kolenati, 1857	*Miniopterus schreibersi* Kuhl
S. euryalis Canestrini, 1885	—
S. javensis Oudemans, 1914	Bat
S. amboinensis Oudemans, 1925	Bat
S. abyssinicus Hirst, 1927	Bat
S. antipodianus Hirst, 1931	Bat
S. novae-hollandiae Hirst, 1931	Bat
S. araguensis Vitzthum, 1931	*Myotis nigricans* Wied
S. ewingia Wharton, 1938	—

Genus **Ancystropus** Kolenati, 1856

Ancystropus zelebori Kolenati, 1856	*Rhinopoma microphyllum* Brunnich
A. (*Meristaspis*) *lateralis* Kolenati, 1856	—
A. aethiopicus Hirst, 1923	*Epomophorus minor* Dobson
A. (*Meristaspis*) *calcaratus* Hirst, 1923	*Pteropus* sp.
A. (*Meristaspis*) *macroglossi* Hirst, 1923	*Macroglossus minimus* Geoffroy

Genus **Periglischrus** Kolenati, 1858

Periglischrus interruptus Kolenati, 1856	*Rhinolophus blasii* Peters
P. hipposideros Kolenati	—
P. asema Kolenati	—
P. caligus Kolenati	—
P. glutinimargo Kolenati	—
P. jheringi Oudemans, 1902	*Vampyrops lineatus* Geoffroy
P. meridensis Hirst, 1927	*Artibeus jamaicensis* Leach

Genus **Halarachne** Allman, 1847

Halarachne halichoeri Allman, 1847	*Halichoerus grypus* Fabricius
H. americana Banks, 1899	*Monachus tropicalis* Gray
H. attenuata Banks, 1910	Seal pup?
H. rosmari Oudemans, 1916	*Odobenus rosmarus*
H. zalophi Oudemans, 1916	*Zalophus californianus*
H. miroungae Ferris, 1925	*Mirounga angustirostris*

Genus **Pneumonyssus** Banks, 1901

Pneumonyssus simicola Banks, 1901	*Pithecus nemestrinus* L.
P. duttoni Newstead & Todd, 1906	*Cercopithecus schmitdi* Matschie
P. congoensis Ewing, 1929	*Papio porcarius* Bodd
P. stammeri Vitzthum, 1930	*Lagothrix infumatus* Spix
P. dinolti Oudemans, 1935	*Macaca mulatta* Zimmerman = *Pithecus rhesus* Audebert
P. procavians Radford, 1938	*Procavia capensis* Pallas
P. caninum Chandler & Ruhe, 1940	*Canis familiaris* L.

Genus **Rhinonyssus** Trouessart, 1894

Rhinonyssus coniventris Trouessart, 1894	*Arenaria interpres* L.
R. levinseni Tragardh, 1904	*Somateria mollisima* L.
R. caledonicus Hirst, 1921	*Uria grylle* L.
R. echinipes Hirst, 1921	*Aegialites hiaticola*
R. neglectus Hirst, 1921	*Calidris maritima*
R. novae-guineae Hirst, 1921	*Craspedophora magnifica*
R. waterstoni Hirst, 1921	*Alca torda* L.
R. orientalis Ewing, 1933	*Lanius nigriceps longicaudatus*

Genus **Rhinonyssoides** Hirst, 1921

Rhinonyssoides trouessarti Hirst, 1921	*Sphecotheres maxillaris*

Genus **Neonyssus** Hirst, 1921

Neonyssus intermedius Hirst, 1921	?

Genus **Neonyssoides** Hirst, 1923

Neonyssoides nucifragae Hirst, 1923	*Nucifraga caryocatactes* L.

Genus **Ptilonyssus** Berlese & Trouessart, 1889

Ptilonyssus nudus Berlese & Trouessart, 1889	*Passer domesticus* L.

Genus **Sternostomum** Berlese & Trouessart, 1889

Sternostomum rhinolethrum Trouessart, 1895	*Anser anser*
S. cryptorhynchum Berlese & Trouessart, 1889	*Passer domesticus* L.

Genus **Entonyssus** Ewing, 1922

Entonyssus halli Ewing, 1922	*Pithyophis melanoleucus* Daudin
E. rileyi Ewing, 1924	*Crotalus durissus*
E. glasmacheri Vitzthum, 1935	*Elaphe quadrivittatus* Holbrook
E. ewingi Hubbard, 1939	*Crotalus cinereous* LeConte
E. vitzthumi Schmidt, 1940	*Pituophis sayi* (Schlegel, 1837) Cope, 1898

Genus **Ophiopneumicola** Hubbard, 1938

Ophiopneumicola bedfordi Radford, 1937	*Dendraspis angusticeps* Smith
O. colubri Hubbard, 1938	*Coluber flagellum flavi-gularis* Hallowell
O. hamertoni Radford, 1939	*Thamnophis sirtalis* L.

Genus **Ixodorhynchus** Ewing, 1922

Ixodorhynchus liponyssoides Ewing, 1922	Snake

Genus **Ixobioides** Fonseca, 1934

Ixobioides butantanensis Fonseca, 1934	*Ophis merremii* Wagler

Genus **Cytolichus** Megnin, 1879

Cytolichus nudus Vizioli, 1870	*Phasianus colchicus* L.
C. banksi Wellman & Wherry, 1910	*Citellus beecheyi beecheyi* Richardson
C. penrosei Weidman, 1917	*Cynomys ludovicianus* Ord
C. hominis Hirst, 1917	Man

Genus **Laminosioptes** Megnin, 1879

Laminosioptes cysticola Vizioli, 1870	—

Genus **Listrophorus** Pagenstecher, 1861

Listrophorus gibbus Pagenstecher, 1861	*Oryctolagus cuniculus* L.
L. leuckarti Pagenstecher, 1861	*Microtus arvalis arvalis* Pallas, 1778
L. pagenstecheri Haller, 1880	*Sciurus vulgaris vulgaris* L., 1758
L. mustelae Megnin, 1885	*Mustela nivalis* L.

Listrophorus dipodicola Tragardh, 1904	*Gerbillus gerbillus gerbillus* Olivier, 1801
L. validus Banks, 1909	Musk rat
L. argentinus Hirst, 1921	*Scapteromys tomentosus* Lichtenstein, 1829
L. frontalis Hirst, 1921	*Oryzomys delticola* Thomas, 1917
L. bothae Hirst, 1923	*Gerbille*
L. brevicaudatus Ullrich, 1939	*Lepus timidus* L.
L. lophuromys Radford, 1940	*Lophuromys sikapusi sikapusi* Temminck, 1853

Genus **Listrophoroides** Hirst, 1923

Listrophoroides aethiopicus Hirst, 1923	*Cricetomys gambianus gambianus* Waterhouse, 1840
L. bathyergians Radford, 1939	*Bathyergus suillus suillus* Schreber, 1782
L. lemniscomys Radford, 1940	*Lemniscomys striatus massaicus* Pagenstecher, 1884
L. mastomys Radford, 1940	*Mastomys coucha erythroleucus* Temminck, 1853
L. tragardhi Radford, 1940	*Rattus norvegicus norvegicus* Berkenhout, 1769
L. dasymys Radford, 1942	*Dasymys* sp.

Genus **Myocoptes** Claparedi, 1869

Myocoptes musculinus Koch, 1844	*Mus musculus musculus* L., 1758
M. criceti Poppe, 1887	*Cricetus cricetus cricetus* L., 1758
M. tenax Michael, 1889	*Microtus arvalis arvalis* Pallas, 1778
M. glirinus Canestrini, 1895	*Glis glis glis* L., 1766
M. hintoni Hirst, 1919	*Sciurus vulgaris vulgaris* L., 1758

Genus **Chirodiscoides** Hirst, 1917

Chirodiscoides caviae Hirst, 1917	*Cavia*

Genus **Labidocarpus** Trouessart, 1895

Labidocarpus rollinati Trouessart, 1895	*Rhinolophus ferrum equinum* Schreber
L. megalonyx Trouessart, 1895	*R. ferrum equinum* Schreber
L. minor Trouessart, 1897	*R. ferrum equinum* Schreber
L. nasicolus Lawrence, 1938	*Rhinolophus augur zuluensis* Andersen

Genus **Myobia** von Heyden, 1826

Myobia musculi Schrank, 1781	*Mus musculus musculus* L., 1758
M. lemnina Koch, 1835	*Microtus agrestis hirtus* Bellamy, 1839
M. brevihamata Haller, 1882	*Mustela nivalis* L.
M. chiropteralis Michael, 1884	*Rhinolophus hipposideros* Bech
M. heteronycha Berlese & Trouessart, 1889	*Asellia tridens* Geoffroy
M. poppei Trouessart, 1895	*Pipistrellus nathusii* Keys & Blasius
M. pantopus Pope & Trouessart, 1895	*Barbastella barbastellus* Schreber
M. affinis Poppe, 1896	*Mus musculus musculus* L., 1758

Myobia claparedei Poppe, 1896	*Sorex araneus* L.
M. elongata Poppe, 1896	*S. araneus* L.
M. ensifera Poppe, 1896	*Rattus norvegicus norvegicus* Berkenhout, 1769
M. michaeli Poppe, 1896	*Crocidura russula* Hermann
M. trouessarti Poppe, 1896	*Potamogale velox* Du Chaillu
M. oudemansi Poppe, 1908	*Muscardinus avellanarius avellanarius* L., 1758
M. lancearia Poppe, 1908	*Apodemus sylvaticus sylvaticus* L., 1758
M. multivaga Poppe, 1908	*Micromys minutus soricinus* Pallas, 1769
M. rollinati Poppe, 1908	*Rhinolophus ferrum equinum* Schreber
M. caudata Banks, 1909	Little brown bat
M. ingens Vitzthum, 1914	*Pachyura etrusca* Savi
M. etheldredae Perkins, 1925	*Pipistrellus pipistrellus* Schreber
M. magna Radford, 1934	*Pteropus giganteus* Brunnich
M. mystacinalis Radford, 1935	*Myotis mystacinus* Kuhl
M. blairi Radford, 1936	*Crocidura cassiteridum* Hinton
M. zibethicalis Radford, 1936	*Ondatra zibethica zibethica* L., 1766
M. plecotia Radford, 1938	*Plecotus auritus* L.
M. pipistrellia Radford, 1938	*Pipistrellus pipistrellus* Schreber
M. noctulia Radford, 1938	*Nyctalus noctula* Schreber
M. davisi Radford, 1938	*Rattus norvegicus norvegicus* Berkenhout, 1769
M. rhinolophia Radford, 1940	*Rhinolophus lobatus* Peters
M. minuta Radford, 1940	Bat
M. jacksoni Radford, 1940	Bat
M. chalinolobus Womersley, 1941	*Chalinolobus gouldi* Gray
M. clara Womersley, 1941	Bat
M. minima Womersley, 1941	*Chalinolobus gouldi* Gray
M. miniopteris Womersley, 1941	*Miniopterus schreibersi* Kuhl

Genus **Psorergates** Tyrrell, 1883

Psorergates simplex Tyrrell, 1883	Mouse
P. ovis Womersley, 1941	Sheep

Genus **Harpyrynchus** Megnin, 1880

Harpyrynchus nidulans Nitzsch, 1818	*Alauda arvensis* L.
H. tabescentium Berthold, 1845	Man
H. crista-galli Berlese & Trouessart, 1889	*Colius striatus*
H. holopus Berlese & Trouessart, 1889	*Passer domesticus* L.
H. pilirostris Berlese & Trouessart, 1889	*Passer domesticus* L.
H. longipilis Banks, 1904	*Loxia* sp.

Genus **Ophioptes** Sambon, 1928

Ophioptes parkeri Sambon, 1928	*Erythrolamprus aesculapii* L.
O. oudemansi Sambon, 1928	*Clelia rustica* Cope

Genus **Geckobia** Megnin, 1878

Geckobia latasti Megnin, 1878	—
G. loricata Berlese, 1892	—
G. tarantulae Tragardh, 1905	*Tarentula annulata*

Geckobia similis Tragardh, 1905	*Hemidactylus turcicus* L.
G. neumanni Berlese, 1910	*Agama colonorum*
G. socotrensis Hirst, 1917	*Pristurus rupestris*
G. clelandi Hirst, 1917	*Gymnodactylus platurus*
G. papuana Hirst, 1917	*Gymnodactylus louisiadensis*
G. boulengeri Hirst, 1917	*Gehyra yunnanensis*
G. malayana Hirst, 1917	*Gymnodactylus pulchellus*
G. indica Hirst, 1917	*Hemidactylus gleadovi*
G. australis Hirst, 1926	*Lygodactylus capensis*
G. gehyrae Hirst, 1926	*Gehyra oceanica*
G. diversipilis Hirst, 1926	*Hemidactylus leschenaulti*
G. gleadoviana Hirst, 1926	*Hemidactylus gleadovi*
G. simplex Hirst, 1926	*Hemidactylus leschenaulti*
G. hindustanica Hirst, 1926	*Hemidactylus leschenaulti*
G. turkestana Hirst, 1926	*Gymnodactylus russovi*
G. bataviensis Vitzthum, 1928	*Hemidactylus frenatus*
G. natalensis Lawrence, 1935	*Lygodactylus capensis*
G. namaquensis Lawrence, 1935	*Pachydactylus namaquensis*
G. hemidactyli Lawrence, 1936	*Hemidactylus tasmani*
G. hewitti Lawrence, 1936	*Pachydactylus maculatus*
G. homopholis Lawrence, 1936	*Homopholis wahlbergii*
G. karrooica Lawrence, 1936	*Oedura karrooica wilmoti*
G. oedurae Lawrence, 1936	*Oe. transvaalica platyceps*
G. ovambica Lawrence, 1936	*Rhotropus barnardi*
G. pachydactyli Lawrence, 1936	*Pachydactylus bibronii*
G. rhoptropi Lawrence, 1936	*Rhoptropus ocellatus*
G. tasmani Lawrence, 1936	*Hemidactylus tasmani*
G. transvaalensis Lawrence, 1936	*Lygodactylus capensis*
G. phyllodactyli Lawrence, 1936	*Phyllodactylus porphyrens*
G. gymnodactyli Womersley, 1941	*Gymnodactylus morio*
G. haplodactyli Womersley, 1941	*Haplodactylus duvaucellii*
G. naultina Womersley, 1941	*Naultinus* sp.

Genus **Geckobiella** Hirst, 1917

Geckobiella texana Banks, 1905	*Sceloporus floridanus*

Genus **Hirstiella** Berlese, 1921

Hirstiella trombidiiformis Berlese, 1921	?

Genus **Pimeliaphilus** Tragardh, 1905

Pimeliaphilus podapolipophagus Tragardh, 1905	*Pimelia* sp.
P. tenuipes Hirst, 1917	*Gondtodes albogularis*
P. insignis Berlese	—

Genus **Pterygosoma** Peters, 1849

Pterygosoma agamae Peters, 1849	*Agama mossambica* Peters
P. inermis Tragardh, 1905	*A. stellio*
P. neumanni Berlese, 1910	*A. colonorum*
P. melanum Hirst, 1917	*A. atra*
P. persicum Hirst, 1917	*A. nupta*
P. bicolor Lawrence, 1935	*Gerrhosaurus flavigularis*
P. gerrhosauri Lawrence, 1935	*G. validus*
P. hystrix Lawrence, 1935	*G. flavigularis*
P. armatum Lawrence, 1936	*Agama hispida armata*
P. bedfordi Lawrence, 1936	*A. atra*
P. hirsti Lawrence, 1936	*A. atra*
P. longipalpe Lawrence, 1936	*A. atra*
P. transvaalensis Lawrence, 1936	*A. atricollis*
P. triangulare Lawrence, 1936	*A. hispida brachyura*
P. aculeatum Lawrence, 1936	*A. hispida aculeata*

Genus **Zonurobia** Lawrence, 1935

Zonurobia circularis circularis Lawrence, 1935	*Platysaurus guttatus*
Z. circularis capensis Lawrence, 1935	*P. capensis*
Z. circularis latior Lawrence, 1935	*Zonurus vittifer*
Z. circularis longipilis Lawrence, 1935	*Platysaurus guttatus*
Z. circularis spiniventer Lawrence, 1935	*P. guttatus minor*
Z. circularis transvaalensis Lawrence, 1935	*P. wilhelmi*
Z. cordylensis Lawrence, 1935	*Zonurus cordylus*
Z. debilipes Lawrence, 1935	*Z. warreni*
Z. montana Lawrence, 1935	*Z. namaquensis*
Z. polyzonensis Lawrence, 1935	*Z. polyzonus*
Z. sanguinea Lawrence, 1935	*Z. coeruleopunctatus*
Z. semilunaris Lawrence, 1935	*Pseudocordylus microlepidotus*
Z. subquadrata Lawrence, 1935	*Zonurus robertsi*
Z. transvaalica Lawrence, 1935	*Z. vandami*

Genus **Ixodiderma** Lawrence, 1935

Ixodiderma inverta Lawrence, 1935	*Pseudocordylus subviridis*
I. lacertae Lawrence, 1935	*Scapteira depressa*
I. pilosa Lawrence, 1935	*Pseudocordylus subviridis*

Genus **Scaphothrix** Lawrence, 1935

Scaphothrix convexa Lawrence, 1935	*Zonurus polyzonus*

HOST LIST

Rattus rattus rattus L.	Black rat
R. norvegicus norvegicus Berkenhout	Brown rat
R. hawaiiensis Stone	Hawaii rat

R. whiteheadi whiteheadi Thomas	Whitehead's rat
Mus musculus musculus L.	House mouse
M. musculus algirus Pomel	Algerian mouse
Gyomys apodemoides Finlayson	Finlayson's mouse
Apodemus sylvaticus sylvaticus L.	Wood mouse
A. agrarius agrarius Pallas	Striped field mouse
Dasymys incomtus helukus Heller	East African swamp rat
Arvicanthis abyssinicus rubescens Wroughton	Uganda unstriped grass rat
Rhabdomys pumilio pumilio Sparrmann	Striped mouse
Hylomys trivirgatus trivirgatus Temminck	Three striped bush mouse
Lemniscomys striatus massaicus Pagenstecher	Massai striped grass rat
L. griselda spinalis Thomas	Striped rat
Aethomys chrysophilus chrysophilus de Winton	African bush rat
Thallomys namaquensis grahami Roberts	Graham's rock mouse
Dephomys defua Miller	African rat
Mastomys coucha erythroleucus Temminck	Multimammate rat
M. coucha hildebrandti Peters	Multimammate rat
Melomys cervinipes littoralis Lönneberg	Scale-tailed rat
M. rufescens rufescens Alston	Mosaic-tailed rat
Lophuromys aquilus aquilus True	Speckled, harsh-furred mouse
L. aquilus zena Dollman	Crest-tailed mouse
L. sikapusi sikapusi Temminck	Brush-furred mouse
Acomys cahirinus Desmarest	Spring mouse
Saccostomus campestris campestris Peters	Pouched rat
Cricetomys gambianus gambianus Waterhouse	Gambian pouched rat
Micromys minutus soricinus Pallas	Harvest mouse
Oryzomys delticola Thomas	Uruguay mouse
O. eliurus Wagner	Mouse
O. subflavus Wagner	Vesper mouse
Peromyscus californicus californicus Gambel	Parasitic mouse
P. eremicus eremicus Baird	Desert mouse
P. truei truei Shufeldt	White-footed mouse
Phodopus roborovskii bedfordiae Thomas	Hamster
Cricetus cricetus cricetus L.	Hamster
Mystromys albicaudatus albicaudatus Smith	White-tailed rat
Akodon olivaceus Waterhouse	Mouse
Reithrodon cuniculoides cuniculoides Waterhouse	Rabbit rat
Holochilus sciureus Wagner	Water rat
H. vulpinus Lichtenstein	Water rat
Neotoma lepida lepida Thomas	Wood rat
Tachyoryctes ruddi ruddi Thomas	Mount Elgon mole rat
Scapteromys tomentosus Lichtenstein	Uruguay mouse
Gerbillus gerbillus gerbillus Olivier	Lesser Egyptian gerbille
Tatera benvenuta benvenuta Hinton & Kershaw	Gerbille
T. brantsi brantsi Smith	Gerbille
Myospalax cansus cansus Lyon	Mole rat

Phenacomys albipes Merriam	Coast mouse
Lemmus obensis obensis Brants	Siberian lemming
Clethrionomys dawsoni dawsoni Merriam	Red-backed mouse
Microtus arvalis arvalis Pallas	Small vole
M. agrestis hirtus Bellamy	Field vole
Arvicola amphibius amphibius L.	Water rat
Ondatra zibethica zibethica L.	Musk rat
Bathyergus suillus suillus Schreber	Cape dune mole
Georychus capensis capensis Pallas	Cape blesmol
Cryptomys hottentotus hottentotus Lesson	Mole rat
Euryzygomatomys spinosus catellus Thomas	Spring rat
Cuniculus paca paca L.	Agouti
Cavia aperea aperea Erxleben	Cavy
Caviella australis australis Geoffroy & D'Arbigny	Cavy
Galea spixii Wagler	Cavy
Sciurus aestuans aestuans L.	South American squirrel
Tamiasciurus hudsonicus richardsoni Bachman	Richardson's red squirrel
Protoxerus stangeri centricola Thomas	Squirrel
Citellus beecheyi beecheyi Richardson	Squirrel
Cynomys ludovicianus ludovicianus Ord	Prairie dog
Muscardinus avellanarius avellanarius L.	Dormouse
Glis glis glis L.	Dormouse
Spalax microphthalmus Guldenstaedt	Mole rat
S. monticola thermaicus Hinton	Mole rat
Blarina brevicauda talpoides	American short-tailed shrew
Sorex araneus L.	Common shrew
Crocidura russula Hermann	Shrew
C. cassiteridum Hinton	White-toothed shrew
Potamogale velox Du Chaillu	Otter shrew
Pachyura etrusca Savi	Musk shrew
Talpa europaea L.	Common mole
Scalops argentatus Aud. & Bach.	Mole
Thalacomys lagotis Reid	Rabbit bandicoot
Solenodon paradoxus Brdt.	Haytian solenodon
Perameles nasuta Geoffroy	Long-nosed bandicoot
Mustela nivalis L.	Common weasel
Gallictis vittata	Weasel
Oryctolagus cuniculus L.	Common rabbit
Lepus timidus L.	Hare
Didelphys aurita Wied	Opossum
Smutsia temmincki Smuts	Scaly ant-eater
Kobus defassa ugandae Neumann	Waterbuck
Procavia capensis Pallas	Cape dassie
Canis familiaris L.	Dog
Macaca mulatta Zimm.	Rhesus monkey
Pithecus nemestrinus L.	Pig-tailed macaque

Circopithecus schmidti Matschie	Putty-nosed guenon
Papio porcarius Bodd.	Chacma baboon
Lagothrix infumatus Spix.	Brown woolley monkey
Lemur mongox var. *albifrons* Petiver	Lemur
Nyctalus noctula Schreber	Noctule bat
Miniopterus schreibersi Kuhl	Long-fingered bat
Rhinolophus ferrum equinum Schreber	Greater horse-shoe bat
R. hipposideros Bech	Lesser horse-shoe bat
R. auryale Blasius	Horse-shoe bat
R. blasii Peters	Horse-shoe bat
R. lobatus Peters	Peters's horse-shoe bat
R. augur zuluensis Andersen	Horse-shoe bat
Myotis daubentonii Kuhl	Daubenton's bat
M. dasycnemus Boie	Mouse-eared bat
M. myotis Borkhausen	Mouse-eared bat
M. nigricans Wied.	South American mouse-eared bat
M. mystacinus Kuhl	Whiskered bat
Rousettus aegyptiaca Geoffroy	Egyptian fruit bat
Nyctinomus brasiliensis Geoffroy	Wrinkled-lipped bat
Pipistrellus pipistrellus Schreber	Pipistrelle bat
P. nathusii Keys & Blasius	Pipistrelle bat
Molossos nasutus Spix.	Wrinkled-lipped bat
Nycticeius humeralis Rafinesque	Rafinesque's evening bat
Liponycteris nudiventris Cretzschmar	Tomb bat
Artibeus jamaicensis Leach	False vampire
Rhinopoma microphyllum Brunnich	Long-tailed bat
Epomophorus minor Dobson	Lesser epauletted bat
Macroglossus minimus Geoffroy	Long-tongued fruit bat
Pteropus giganteus Brunnich	Indian fruit bat
P. edulis Geoffroy	Fruit bat
Plecotis auritus L.	Long-eared bat
Asellia tridens Geoffroy	Trident bat
Barbastella barbastellus Schreber	Barbastelle bat
Chalinolobus gouldi Gray	Gould's bat
Eptesecus serotinus Schreber	Serotine bat
Vampyrops lineatus Geoffroy	Bat
Tadarida brasiliensis Geoffroy	Free-tailed bat
T. mexicana Saussure	Free-tailed bat
Gallus domesticus	Fowl
Passer domesticus L.	House sparrow
Otus asio asio	American Scops owl
Dendrocopus major	Great spotted woodpecker
D. cardinalis	Woodpecker
D. fuscescens lepidus	Woodpecker
Riparia riparia L.	Sand martin
Cypselus affinis	Swift

Arenaria interpres L.	Turnstone
Somateria mollisima L.	Eider duck
Craspidophora magnifica	—
Uria grylle L.	Black guillemot
Alca torda L.	Razorbill
Aegialites hiaticola	King plover
Calidris maritima	Purple sandpiper
Lanius nigriceps longicaudatus	Shrike
Sphecotheres maxillaris	Australian oriole
Nucifraga caryocatactes L.	Thick-billed nutcracker
Progne subis	Martin
Colius striatus	Mouse bird
Colaptes cafer	—
Elaphe obsoleta	Pilot black snake
E. quadrivittatus Holbrook	Chicken snake
E. guttata	Corn snake
Coluber viridiflavus	—
Thamnophis ordinoides ordinoides B. & G.	Cooper's snake
T. sirtalis	North American garter snake
Pithyophis melanoleucus Daudin	Pine snake
Crotalus durissus	Rattlesnake
C. cinereous Le Conte	Rattlesnake
Pituophis sayi Schlegel	Bull snake
Ophis merremii Wagler	Merrem's Boipeva snake
Erythrolamprus aesculapii L.	—
Clelia rustica Cope	—
Dendraspis angusticeps Smith	Green mamba
Lampropeltis calligaster	King snake
Drymarchon corais melanurus	Gopher snake
Lacerta agilis L.	Sand lizard
L. viridis	Green lizard
Sceloporus graciosus	Lizard
S. floridanus	Lizard
Scapteira depressa	Lizard

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ADDENDA

The publication by Dr H. Graf Vitzthum (1935) of the paper 'Milben aus der Nasenhöhle von Vögeln' in *J. Ornith.* **83**, 563–87, necessitates some alterations to the family Rhinonyssidae, and I give below the grouping as reconstituted by Vitzthum.

Genus **Sternostomum** Trouessart, 1895

Sternostomum rhinolethrum Trouessart, 1895	*Anser anser*
S. levinseni Tragardh, 1904	*Somateria mollisima* L.
S. calidonicum Hirst, 1921	*Uria grylle* L.
S. waterstoni Hirst, 1921	*Alca torda* L.
S. technaui Vitzthum, 1935	*Cinclus cinclus aquaticus*

Genus **Sternostoma** Berlese & Trouessart, 1889

Sternostoma cryptorhynchum Berlese & Trouessart, 1889	*Passer domesticus* L.

Genus **Rhinonyssus** Trouessart, 1894

Rhinonyssus coniventris Trouessart, 1894	*Arenaria interpres* L.
R. neglectus Hirst, 1921	*Calidris maritima*
R. echinipes Hirst, 1921	*Aegialites hiaticola*
R. novae-guineae Hirst, 1921	*Craspedophora magnifica*
R. nitzschi Giebel, 1871	*Caprimulgus europaeus*
R. squamosus Vitzthum, 1935	*Sericotes holosericeus*

Genus **Rhinonyssoides** Hirst, 1921

Rhinonyssoides trouessarti Hirst, 1921	*Sphecotheres maxillaris*

Genus **Neonyssus** Hirst, 1921

Neonyssus intermedius Hirst, 1921	—
N. nucifragae Hirst, 1923	*Nucifraga caryocatactes* L.

Genus **Ptilonyssus** Berlese & Trouessart, 1889

Ptilonyssus echinatus Berlese & Trouessart, 1889	*Hirundo rustica*
P. nudus Berlese & Trouessart, 1889	*Passer domesticus* L.
P. stresemanni Vitzthum, 1935	*Procnias alba* (=*Chasmorhynchus niveus*)

Genus **Ptilonyssoides** Vitzthum, 1935

Ptilonyssoides triscutatus Vitzthum, 1935	*Merops apiaster*

VARIATION IN GAMETOCYTE PRODUCTION IN A STRAIN OF *PLASMODIUM RELICTUM* IN CANARIES

By ANN BISHOP, Sc.D.,* *From the Molteno Institute, University of Cambridge*

(With 2 Figures in the Text)

Huff & Gambrell (1934), and Gambrell (1937) observed that, when *Plasmodium cathemerium* was passaged from canary to canary for a long period, by inoculation of blood from acutely infected birds, the number of gametocytes produced in each infection gradually decreased, though in two strains only did they disappear completely.

We have, in the Molteno Institute, a strain of *P. relictum*, the gift of the late Dr Roehl of Elberfeld, Germany, which, since its arrival here on 9 December 1927, has been transmitted through canaries (*Serinus canarius*) by blood inoculation. In the course of research upon the chemotherapy of malaria this strain has been studied in large numbers of untreated control birds, at all seasons of the year. Tate & Vincent (1934) observed that the development of gametocytes was irregular in this strain, for whereas in some birds no gametocytes could be found throughout the period of acute infection, in others they were numerous. Dr Tate told me that he had noticed a tendency for a greater number of gametocytes to be formed, during the acute attack, in birds inoculated in summer than in winter. I therefore decided to try to discover by differential counts of asexual parasites and gametocytes in birds inoculated at all seasons of the year, whether such a seasonal variation in gametocyte production could be proved; or whether the number of gametocytes produced in a series of birds infected over a long period by the inoculation of blood from acutely infected birds gradually decreased as Gambrell had found in *P. cathemerium*.

Canaries were infected by the injection of 0·3 c.c. of heavily infected blood in citrate saline solution into the pectoral muscle, the blood being taken from the leg vein of the donor bird. Throughout the period of the experiment (two years) the strain was passaged from acutely infected birds, and never from birds in which the infection had become chronic. Parasites usually appeared in the peripheral blood on the 5th or 6th day after inoculation, and blood films were made, between 10 and 11 a.m., on the 5th and every succeeding day during the period of acute infection. The films were stained with Giemsa's stain. A metal disk with a square aperture in the centre was used in the eyepiece of the microscope to facilitate the counting of corpuscles and parasites.

In order that the intensity of infection could be compared in different birds the number of parasites per 1000 red blood corpuscles was counted on each day during the acute attack, which usually lasted 4–9 days. Counts were made upon birds inoculated each month during two years beginning November 1938. As, in the interests of economy, untreated control birds from experiments upon chemotherapy were used, the number of birds upon which the counts were made varied from month to month, the total over the two years being 91. Intensity of infection varied greatly from bird to bird, but no fatal infection occurred amongst the 91 birds studied. The heaviest infection observed in this series had a maximum of 520 parasites per 1000 red blood corpuscles, and the lightest 11; but infections with a maximum of 90 to 170 parasites per 1000 red blood corpuscles were

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most frequently encountered. Wide variations in the intensity of infection were found amongst birds inoculated with blood from the same donor bird; thus the maximum number of parasites per 1000 corpuscles in each of three birds inoculated from the same donor bird on 10 January 1939 was 206, 40 and 18, whilst in each of three birds inoculated on 30 January 1939 from another donor bird it was 386, 261 and 80.

The monthly average of the maximum number of parasites per 1000 corpuscles was determined. A comparison of these monthly averages (Fig. 1) showed that there was no seasonal variation in the intensity of acute infection, though great variation might occur from month to month.

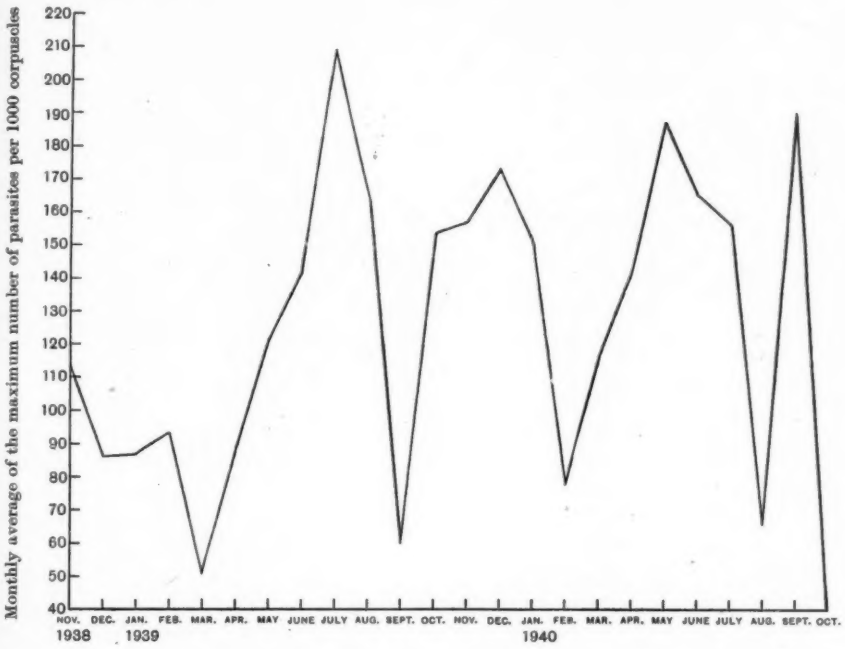

Fig. 1. Monthly average of the maximum number of parasites per 1000 corpuscles from November 1938 to October 1940.

Gametocytes frequently were found on the day on which asexual parasites appeared in the peripheral blood, and occasionally before this. The ratio of mature gametocytes to asexual parasites was determined in all the 91 birds, by counting the number of gametocytes per 500 asexual parasites on each day throughout the period of acute infection. The monthly average of mature gametocytes per 500 parasites was calculated. The proportion of gametocytes to red blood corpuscles was also found, and the monthly average obtained, the result being expressed as the ratio of corpuscles to gametocytes.

The greatest proportion of gametocytes to corpuscles did not necessarily occur at the peak of infection, nor on the day when the proportion of gametocytes to asexual parasites was greatest; in some birds it occurred one day before the peak in development of asexual forms, whereas in others it occurred one or two days later. Huff (1927) found that in

P. cathemerium the maximum number of gametocytes occurred one or two days later than that of the total parasites, whereas in the same species Shah (1934) found that the maximum number of gametocytes and asexual forms occurred simultaneously.

The number of gametocytes formed varied widely from bird to bird, but the rate of gametocyte production in this strain of *P. relictum* was never heavy. The heaviest gametocyte infection in any of the 91 birds was 1 gametocyte per 54 corpuscles, and the greatest proportion of gametocytes to asexual parasites was 1 : 9. Heavy infections of asexual forms were not necessarily accompanied by large numbers of gametocytes (Table 1). This observation was in agreement with that of Huff & Gambrell (1934), who failed to find any correlation, in *P. cathemerium*, between the intensity of infection and the number of gametocytes formed.

Table 1

Serial no. of bird	Date of inoculation	Max. no. of asexual parasites per 1000 corpuscles	Max. no. of gametocytes per 500 parasites	Ratio of gametocytes to corpuscles
3250	5. viii. 39	119	9	1 : 467
2957	14. xi. 38	115	1	1 : 4348
2974	10. i. 39	40	2	1 : 8569
3061	18. iv. 39	38	6	1 : 2188
3066	18. iv. 39	44	14	1 : 811
3540	13. ii. 40	105	1	1 : 7692
3624	15. iv. 40	104	7	1 : 687
3120	8. v. 39	62	13	1 : 620
3867	9. x. 40	60	1	1 : 8333
3083	24. iv. 39	237	11	1 : 212
3789	16. ix. 40	243	1	1 : 12,500
3664	18. v. 40	520	25	1 : 54

Blood from birds rich in gametocytes did not necessarily produce infections equally rich when inoculated into clean birds. Thus blood from a bird in which the maximum number of gametocytes was 1 gametocyte per 54 red blood corpuscles produced an infection with a maximum of 1 gametocyte per 1474 corpuscles. A single sample of blood, if inoculated at the same time into two or more birds, kept under similar conditions, often produced infections which differed considerably in the number of gametocytes formed. Thus of two birds inoculated with blood from one donor bird one had an infection with a maximum of 1 gametocyte per 375 corpuscles, whilst in the other the maximum was 1 gametocyte per 6250 corpuscles. Of two birds inoculated from a donor bird in which the maximum rate of gametocyte infection was 1 gametocyte per 306 red blood corpuscles, one had a maximum of 1 gametocyte per 666 corpuscles and the other 1 gametocyte per 12,500 corpuscles.

In order to discover whether variation in intensity of infection and in gametocyte production was due to difference in age of the hosts, four canaries were inoculated, in August 1942, each with 0·3 c.c. of a mixture of citrate saline solution and blood taken from a bird which had a maximum infection of 178 parasites per 1000 corpuscles and a ratio of 1 gametocyte to 468 corpuscles. Two of the birds inoculated had been bred in the Institute from the same clutch of eggs and were two months old at the time of inoculation, whereas the other two birds, bought from a dealer, were old birds, as judged by the condition of their legs and feet.

In so far as could be judged from these four observations (Table 2) the intensity of infection with *P. relictum* and the number of gametocytes produced were not correlated

with the age of the host, but rather appeared to vary with the reactions of individual birds irrespective of age or relationship.

Table 2

	Parasites per 1000 red blood corpuscles	Ratio of gametocytes to red blood corpuscles
A. Old bird	103	1 : 809
B. Old bird	144	1 : 385
C. Young bird	212	1 : 235
D. Young bird	50	1 : 6410

In 6 of the 91 birds examined no gametocytes were found though blood films were examined exhaustively on each day during the period of acute infection. These birds

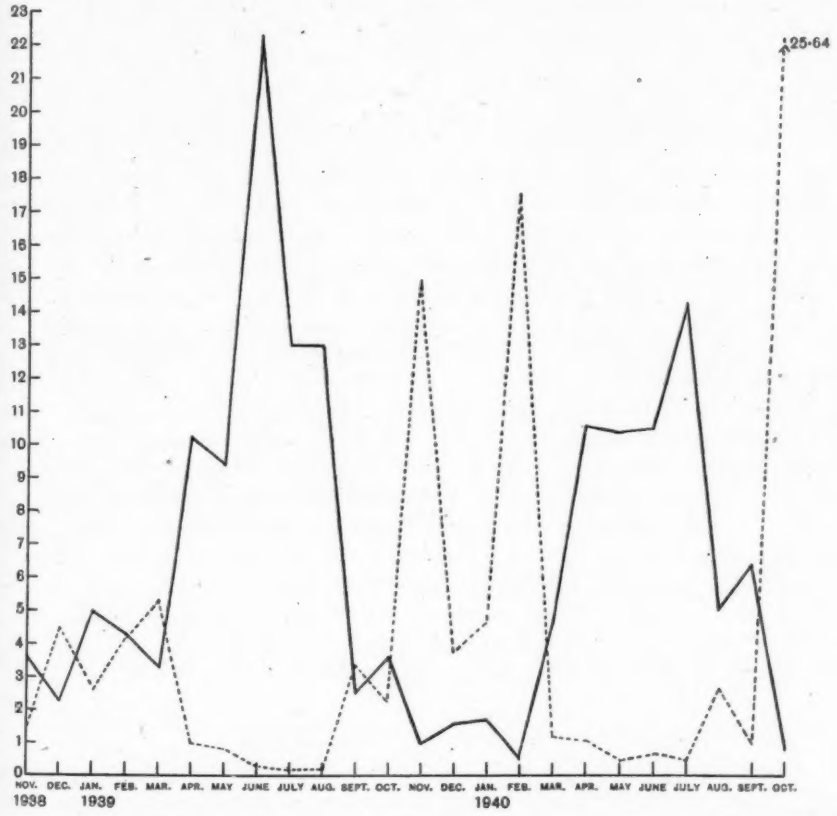

Fig. 2. Monthly average of the maximum number of gametocytes formed from November 1938 until October 1940. —— ratio of average number of gametocytes to 500 parasites. ----- average number of corpuscles per gametocyte expressed in thousands.

were inoculated in the autumn and winter months, from and including October to March. Gametocytes were found in all birds inoculated during the summer months. The birds in which no gametocytes were found had infections of less than average intensity. When blood from one of these gametocyteless birds was inoculated into two clean birds gametocytes appeared in both the infections produced.

A comparison of the monthly average of the maximum number of gametocytes per 500 parasites, during the two years over which these observations were made (Fig. 2), showed that the average was higher in April until July or August than in the remaining part of the year, though in 1939 the greatest monthly average, that of June, was much greater than that of 1940. In both years the proportion of gametocytes to asexual parasites dropped sharply during the autumn months. When the numbers of gametocytes formed were assessed in terms of red blood corpuscles it was found that the monthly averages fluctuated much more widely than when they were assessed in proportion to asexual parasites, but they were most numerous (i.e. the number of red blood corpuscles per gametocyte was lowest) from April until August (1939) or March until July (1940) than at other times of the year.

Discussion

From observations upon several strains of *Plasmodium cathemerium*, Gambrell (1937) is of the opinion that 'gametocyte production is an inherent quality of the parasite, rather than a function dependent solely on environmental stimuli', and that different strains vary in their ability to form gametocytes. That some strains of *P. falciparum* produce many gametocytes whereas others produce few had been noted by Marchoux (1922). Korteweg (1930) also found a difference in degree of gametocyte production in strains of *P. vivax*. But though a high or low rate of gametocyte production may be characteristic of a strain of *Plasmodium* taken over a long period, the variation in number of gametocytes of *P. relictum* formed in individual birds inoculated with blood from the same source suggests that some factor in the bird influences the number of gametocytes produced in each individual infection. If such be the case this factor must be independent of that which determines the intensity of total infection, since no correlation has been observed between intensity of total infection and the number of gametocytes produced. The fact that after the peak of infection the decline in number of asexual forms was accompanied by that of the gametocytes indicated that gametocyte production was not instigated by the development of immunity to the infection in the host. These observations agree with those of Garnham (1931–2) who, in *P. falciparum*, failed to find any correlation between the number of crescents and asexual forms, or any indication that the development of crescents was correlated with the development of immunity in the host. The inoculation of serum from patients heavily infected with crescents did not cause an early appearance of these forms in new infections.

Conclusions

The number of gametocytes produced in a strain of *Plasmodium relictum*, when passaged for two years through canaries by blood inoculation from acutely infected birds, did not undergo a gradual decrease, as Gambrell had found in *P. cathemerium*. There was a seasonal fluctuation in the production of gametocytes, as the average number produced from April until July or August was higher than at other times of the year. The number of gametocytes formed in birds inoculated from the same source varied widely, irrespective of the intensity of infection, or the age of the host.

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